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Cetacean habitats in the northern Gulf of Mexico

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Abstract–Surveys were conducted in the northern Gulf of Mexico during the spring seasons of 1992, 1993, and 1994 to determine the distribution, abundance, and habitat preferences of oceanic cetaceans. The distributions of bottlenose dolphins (*Tursiops truncatus*), Risso's dolphins (*Grampus griseus*), *Kogia* spp. (pygmy [*Kogia breviceps*] and dwarf sperm whales [*Kogia sima*]), pantropical spotted dolphins (*Stenella attenuata*), and sperm whales (*Physeter macrocephalus*) were examined with respect to depth, depth gradient, surface temperature, surface temperature variability, the depth of the 15°C isotherm, surface chlorophyll concentration, and epipelagic zooplankton biomass. Bottlenose dolphins were encountered in two distinct regions: the shallow continental shelf (0–150 m) and just seaward of the shelf break (200–750 m). Within both of these depth strata, bottlenose dolphins were sighted more frequently than expected in regions of high surface temperature variability which suggests an association with ocean fronts. Risso's dolphins were encountered over the steeper sections of the upper continental slope (200–1000 m), whereas the *Kogia* spp. were sighted more frequently in waters of the upper continental slope that had high zooplankton biomass. The pantropical spotted dolphin and sperm whale were similarly distributed over the lower continental slope and deep Gulf (>1000 m), but sperm whales were generally absent from anticyclonic oceanographic features (e.g. the Loop Current, warm-core eddies) characterized by deep occurrences of the 15°C isotherm. Habitat partitioning, high-use areas, species accounts, environmental sampling limitations, and directions for future habitat work in the Gulf of Mexico are discussed.

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Studies of cetacean distribution in the northern Gulf of Mexico have largely relied on stranding, opportunistic sighting, and limited survey data (Jefferson and Schiro, 1997) until recently (Mullin et al., 1994; Davis and Fargion[1]; Davis et al.[2]). During the past decade, both aerial and shipboard assessment surveys in the oceanic (>200 m depth) northern Gulf have identified and characterized the abundance and distribution of 20 species of cetaceans, all but one of which were odontocetes (Mullin et al., 1994; Mullin and Hansen, 1999; Hansen et al.[3]; Mullin and Hoggard[4]). Only two of these species, the bottle-

[1] Davis, R. W., and G. S. Fargion. 1996. Distribution and abundance of cetaceans in the north-central and western Gulf of Mexico: final report, vol. I: executive summary. U.S. Department of the Interior, Minerals Management Service, OCS Study MMS 96-007, 29 p. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

[2] Davis, R. W., W. E. Evans, and B. Würsig. 2000. Cetaceans, sea turtles and seabirds in the northern Gulf of Mexico: distribution, abundance and habitat associations, vol. I: executive summary. U.S. Department of the Interior, Geological Survey, Biological Resources Division, USGS/BRD/CR-1999-0006 and Minerals Management Service, OCS (outer continental shelf) Study MMS 2000-003, 27 p. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

[3] Hansen, L. J., K. D. Mullin, T. A. Jefferson, and G. P. Scott. 1996. Visual surveys aboard ships and aircraft. *In* Distribution and abundance of cetaceans in the north-central and western Gulf of Mexico: final report, vol. II: technical report (R. W. Davis and G. S. Fargion, eds.), p. 55–128. U.S. Department of the Interior, Minerals Management Service, OCS Study MMS 96-007. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

[4] Mullin, K. D., and W. Hoggard. 2000. Visual surveys of cetaceans and sea turtles from aircraft and ships. *In* Cetaceans, sea turtles and seabirds in the northern Gulf of Mexico: distribution, abundance and habitat associations, vol. II: technical report (R. W. Davis, W. E. Evans, and B. Würsig, eds.), p. 111–171. U.S. Department of the Interior,

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nose dolphin (*Tursiops truncatus*) and Atlantic spotted dolphin (*Stenella frontalis*), occur regularly over the continental shelf (Fritts et al., 1983; Mullin et al., 1994; Davis et al., 1998). In contrast, the oceanic Gulf supports a wide diversity of cetacean species by potentially supplying a large number of ecological niches. Although predator avoidance, interspecific competition, and reproductive strategies all affect cetacean distribution to some extent, energetic budget studies indicate that most cetaceans must feed every day (Smith and Gaskin, 1974; Lockyer, 1981; Kenney et al., 1985; CETAP[5]) and thus habitat is assumed to be primarily determined by the availability of food (Kenney and Winn, 1986). The distribution of the oceanic species, then, is presumably linked to the rather dynamic oceanography of the Gulf of Mexico through physical-biological interactions and trophic relationships between phytoplankton, zooplankton, micronekton, and cetacean prey species. For most cetaceans in the Gulf of Mexico, specific prey species are not known but likely include epi- and mesopelagic fish and cephalopods (Fitch and Brownell, 1968; Perrin et al., 1973; Würtz et al., 1992; Clarke, 1996).

The physical and biological oceanography of the northern Gulf of Mexico is highly variable in both space and time. The eastern Gulf contains the Loop Current, an extension of the Gulf Stream system that enters the Yucatan Channel, turns anticyclonically, and exits through the Straits of Florida. The northward penetration of the Loop Current into the Gulf of Mexico normally varies between 24° and 28°N on a quasi-annual basis (Sturges and Evans, 1983). Cold, potentially biologically rich, upwelling features are frequently found at the edge of the Loop Current and often develop into cyclonic, cold-core eddies (Vukovich et al., 1979; Maul et al., 1984; Vukovich and Maul, 1985; Richards et al., 1989). Large, anticyclonic, warm-core eddies can shed from the Loop Current during its maximum northerly penetration into the Gulf (Cochrane 1972; Hurlburt and Thompson, 1982) after which they move slowly westward at an average speed of 5 km/day. More than one of these warm-core eddies can be found in the western Gulf of Mexico because their translation (net) speed and decay are slow (Elliot, 1982). During their transit from the eastern to western Gulf of Mexico, these warm-core features can also have associated cyclonic features at their peripheries which are biologically productive (Biggs, 1992). Another major source of nutrients that can drive primary productivity in the oceanic Gulf is the Mississippi River. The Mississippi River Delta protrudes into the Gulf in a region where the continental shelf is narrow and the continental slope is steep. The river's nutrient-rich fresh water plume extends over the deep Gulf and supports high rates of primary productivity and large standing stocks of chlorophyll and zooplankton biomass (El-Sayed, 1972; Dagg et al., 1988; Ortner et al., 1989).

Our study examines the distribution of five commonly encountered cetacean species or species groups in the northern Gulf of Mexico with respect to several physical, biological, and physiographic variables. These species are the bottlenose dolphin, Risso's dolphin (*Grampus griseus*), *Kogia* spp. (pygmy [*Kogia breviceps*] and dwarf sperm whale [*Kogia sima*]), pantropical spotted dolphin (*Stenella attenuata*) and sperm whale (*Physeter macrocephalus*). The environmental and cetacean survey data for our study were collected by the U.S. National Marine Fisheries Service. Subsets of these data have been analyzed by Baumgartner (1997) to characterize the distribution of Risso's dolphins with respect to the physiography of the northern Gulf of Mexico and by Davis et al. (1998) to describe cetacean habitats over the continental slope in the northwestern Gulf. One of the major objectives of these surveys was to help assess the impact of large-scale oil and gas exploration and development in the northern Gulf of Mexico on cetaceans. An understanding of the habitat preferences of each of these species will greatly improve management and conservation efforts by providing a context for interpreting future anthropogenic influences on cetacean distribution.

Materials and methods

Data collection and treatment

We examined the distribution of each cetacean species with respect to seven environmental variables (Table 1) to characterize habitat. These variables were selected because they represent specific oceanographic or physiographic features or conditions. Depth and depth gradient (sea floor slope) were included to represent the physiography of the Gulf of Mexico because the distribution of some cetaceans has been associated with specific topographic features in the Gulf (Baumgartner, 1997; Davis et al., 1998) and elsewhere (Evans, 1975; Hui, 1979, 1985; Selzer and Payne, 1988; CETAP[5]; Dohl et al.[6]; Dohl et al.[7]; Green et al.[8]). A com-

[4] (*continued from previous page*) Geological Survey, Biological Resources Division, USGS/BRD/CR-1999-0006 and Minerals Management Service, OCS Study MMS 2000-003. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

[5] CETAP (Cetacean and Turtle Assessment Program). 1982. A characterization of marine mammals and turtles in the mid- and north Atlantic areas of the U.S. outer continental shelf. U.S. Department of the Interior, Bureau of Land Management, contract AA551-CT8-48. 584 p. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161.]

[6] Dohl, T. P., K. S. Norris, R. C. Guess, J. D. Bryant, and M. W. Honig. 1978. Summary of marine mammal and seabird surveys of the Southern California Bight area 1975–78, vol. III: Investigators' Reports, part II: Cetacea of the Southern California Bight. U.S. Department of the Interior, Bureau of Land Management, Contract AA550-CT7-36, 414 p. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161.]

[7] Dohl, T. P., R. C. Guess, M. L. Duman, and R. C. Helm. 1983. Cetaceans of central and northern California, 1980–1983. Status, abundance and distribution. U.S. Department of the Interior, Minerals Management Service, contract 14-12-0001-29090, 284 p. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161.]

mon measure of bottom relief, contour index (Evans, 1975), was omitted because it does not distinguish between significantly different topographies in the northern Gulf of Mexico (Baumgartner, 1997). Many oceanographic features, such as eddies or river discharge, have strong sea surface temperature signatures, whereas areas where different water masses abut (frontal zones) are often characterized as regions of high surface temperature variability. Mesoscale warm-core eddies in the Gulf of Mexico are easily detected in hydrographic transects by the deep occurrence of the 15°C isotherm. Finally, surface chlorophyll concentration and zooplankton biomass represent rough measures of the standing stocks on which higher trophic consumers might feed.

Table 1

Environmental variables used in the habitat analyses.

Variable	Source	Units
Depth	digital bathymetry	m
Depth gradient	digital bathymetry	m/1.1 km
Surface temperature	thermosalinograph	°C
Surface temperature standard deviation	infrared satellite imagery	°C
Depth of 15°C isotherm	CTD and XBT casts	m
Surface chlorophyll concentration	surface samples	mg/m^3
Zooplankton biomass	oblique bongo tows	$cc/100\ m^3$

Cetacean surveys were conducted during the spring seasons of 1992, 1993, and 1994 from NOAA Ship *Oregon II* in the Gulf of Mexico approximately north of a line connecting Brownsville, Texas, and Key West, Florida, and primarily in waters deeper than 200 m (Fig. 1). Sighting data were collected with 25× binoculars and standard line-transect survey methods for cetaceans (e.g. Barlow, 1995; Hansen et al.[3]). Time and the ship's position were recorded automatically every two minutes, and at regular intervals the survey team recorded ancillary data, such as sea state, sighting conditions, and effort status. These ancillary data were appended to the time and position records. Environmental data were extracted from the appropriate data sets (discussed below) and also appended to the time and position records. These records comprise the effort data set which provides a complete history of the sighting conditions, survey effort, and environmental observations. The cetacean sighting records were also appended with the environmental and ancillary data and collectively represent the cetacean sighting data set.

Surface temperature was recorded at one-minute intervals with a flow-through thermosalinograph (SeaBird Electronics, Inc, Bellevue, WA). The temperature measurements were low-pass filtered to reduce high frequency and high wave number variability. The filter was a simple 5-min running mean which, at an average vessel speed of 5 m/s (10 knots), is equivalent to averaging over 1.5 km.

Conductivity, temperature, and depth (CTD) or expendable bathythermograph (XBT) casts were conducted every 55 km (30 nmi) along the survey transect. CTD casts were generally made to 500 m or just off the sea floor, whichever was shallower. XBT probes capable of operating to depths of 200 to 1000 m were used in appropriate depths. Surface water samples were collected every 55 km and chlorophyll *a* was measured in these samples by using fluorometric and spectrophotometric techniques described in Strickland and Parsons (1972) and Jeffery and Humphrey (1975). Plankton tows were also conducted at 55-km intervals by using a 61-cm diameter bongo equipped with 0.333-mm mesh nets and flowmeters. The nets were towed obliquely from 200 m or just off the sea floor, whichever was shallower. Samples from one of the bongos were analyzed by the Polish Sorting and Identification Center in Szczecin, Poland. Zooplankton biomass was computed as the ratio of the displacement volume of the sample after organisms larger than 2.5 cm were removed (after Smith and Richardson, 1977) to the volume of water filtered during the tow.

Remotely sensed sea surface temperature (SST) data from the advanced very high resolution radiometer (AVHRR) carried aboard the National Oceanic and Atmospheric Administration (NOAA) polar orbiting environmental satellites were acquired from the U.S. National Environmental, Satellite and Data Information Service. The raw, level 1B data from the NOAA 9, 10, and 11 satellites were warped to a $0.01° \times 0.01°$ linear latitude-longitude projection by using the supplied satellite navigation information, coregistered to a digital coastline and converted to sea surface temperatures by using separate day and night multichannel SST equations. Because of the lower accuracy and relative paucity of the satellite-derived SST data, the *in-situ* surface temperature from the shipboard thermosalinograph was used in the analyses of cetacean habitat. However, these remotely sensed data are well suited to detecting horizontal gradients in SST due to their synoptic coverage. These gradients are often resolved by using digital image gradient operators (e.g. Sobel, Prewitt, or Roberts operators), but we chose another approach after Smith et al. (1986). Because horizontal gradients in SST can be measured as horizontal variability, we computed the standard deviation of the remotely sensed SST within a 10-km radius of each transect and sighting position.

Water depth was extracted from a digital bathymetric data set compiled from NAVOCEANO's DBDB5 5-minute × 5 minute gridded bathymetry, National Ocean Service's high

[3] Green, G. A., J. J. Brueggeman, R. A. Grotefendt, C. E. Bowlby, M. L. Bonnell, and K. C. Balcomb III. 1992. Cetacean distribution and abundance off Oregon and Washington, 1989–1990. *In* Oregon and Washington marine mammal and seabird surveys (J. J. Brueggeman, ed.), p. 1–100. U.S. Department of the Interior, Minerals Management Service, contract 14-12-0001-30426. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161.]

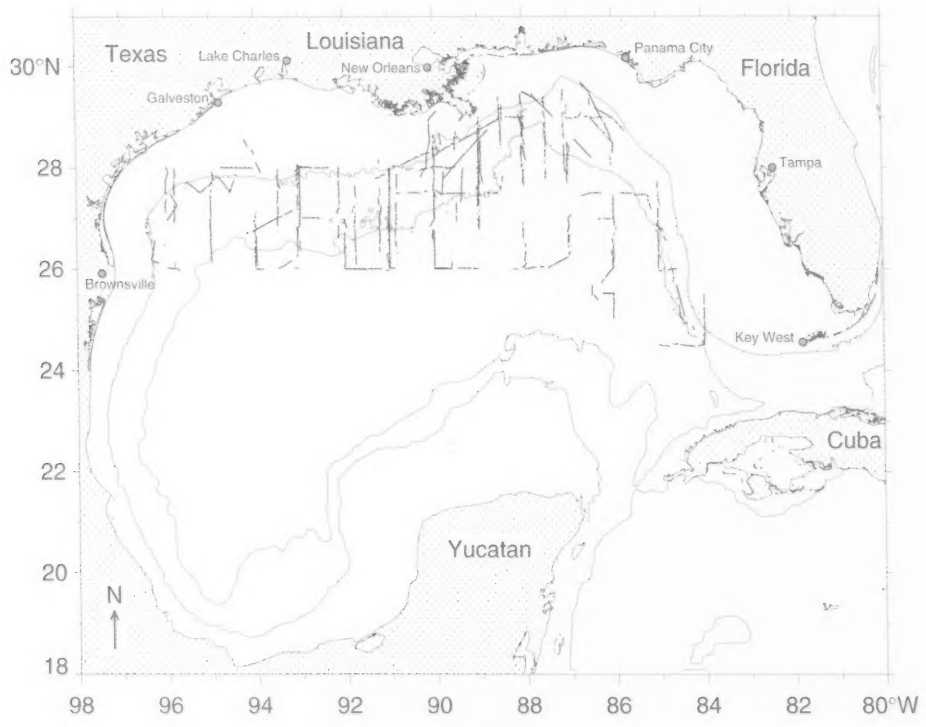

Figure 1

Map of shipboard surveys transects conducted by NOAA Ship *Oregon II* in the spring seasons of 1992, 1993, and 1994. Only transects conducted during active searches for cetaceans during adequate sighting conditions are shown. The 200-m and 2000-m isobaths are indicated in gray.

resolution coastal bathymetric data set and Texas A&M University's digitized bathymetric charts (Herring[9]). This depth data set was provided on a 0.01° × 0.01° linear latitude-longitude grid with a nominal resolution of 1.1 km for the entire Gulf of Mexico. Depth gradient or sea floor slope was derived from the depth grid by using a 3 × 3 pixel Sobel gradient operator. The resulting product had the same base resolution and spatial coverage as the bathymetry data set. For descriptive purposes, the following physiographic terms will be used to denote specific depth ranges or features: continental shelf (0–200 m), shelf break (~200 m), continental slope (200–2000 m), upper continental slope (200–1000 m), lower continental slope (1000–2000 m), and deep Gulf (>2000 m).

A single descriptor of the vertical temperature structure in the upper ocean was selected to quantify the influence of mesoscale features such as eddies on cetacean distribution. Reilly (1990) chose the depth of the 20°C isotherm as an approximate indicator of thermocline depth in his study of cetacean habitat in the eastern tropical Pacific. We used a similar approach by extracting the depth of the 15°C isotherm from each CTD and XBT profile. This variable is not intended to represent the depth of the thermocline, however. The low-frequency, large-scale temperature variability along this isotherm is associated with the mesoscale features of interest and it occurs deep enough that it never reaches the sea surface during the spring in the northern Gulf of Mexico.

The discrete samples of the depth of the 15°C isotherm, surface chlorophyll concentration and zooplankton biomass from each cruise leg (9–17 days in duration) were interpolated on a regular 0.1° × 0.1° linear latitude-longitude grid by using the kriging method (Golden Software, 1994). Surface chlorophyll was log-transformed before interpolation because the observed chlorophyll concentrations had a log-normal distribution and spanned several orders of magnitude (0.02–13.02 mg/m^3). The interpolation method provided consistent results when compared with other data sets (e.g. Fig. 2). Because no interpolation method will capture the true spatial structure of these variables, the accuracy of the interpolated values in the effort and sighting datasets is undoubtedly low. Despite these errors, however, the horizontal variability associated

[9] Herring, H. J. 1993. A bathymetric and hydrographic climatological atlas for the Gulf of Mexico (draft report). U.S. Department of the Interior, Minerals Management Service, contract 14-12-0001-30631, 191 p. [Available from National Technical Information Service, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, VA 22161.]

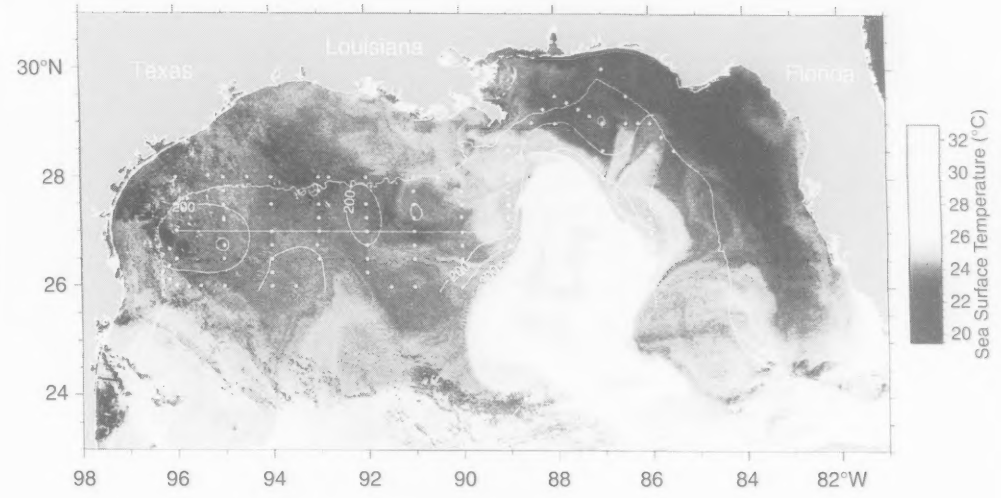

Figure 2

Sea surface temperature of the northern Gulf of Mexico derived from remotely sensed AVHRR data collected between 21 and 23 May 1993. Image is a histogram-equalized, warmest-pixel composite of data derived from three satellite passes with some cloud contamination south of 24.5°N and also west of 93°W. CTD and XBT stations are indicated as filled circles and the contours represent the depth of the 15°C isotherm computed from the CTD and XBT casts collected between 19 May and 1 June 1993. The line along 27°N indicates the parallel from which data were extracted for Figure 3. The 200-m isobath is shown.

with mesoscale oceanographic features is much larger than these errors and therefore the interpolated fields represent these features reasonably well (e.g. Fig. 2).

The base unit of effort for this study was defined as 1 km of actively surveyed transect during adequate sighting conditions. To conform to this definition, each contiguous transect in the effort data set was broken into 1-km linear sections and all the environmental variables measured along each 1-km section were averaged. This provided a single set of observed environmental variables for each unit of effort. Only those 1-km sections that were actively surveyed (i.e. those where the observers were on-effort) during adequate sighting conditions (defined as Beaufort sea states of 3 or less) were used for analysis. Similarly, only those cetacean sightings that occurred while observers were on-effort and in Beaufort sea states of 3 or less were used for analysis. All of the following analyses were conducted on cetacean group sightings and therefore do not account for group size.

Some portions of the described data have been previously published by Davis et al. (1998) and Baumgartner (1997). Davis et al. (1998) examined cetacean habitat in the northwestern Gulf of Mexico with respect to a variety of physical oceanographic and physiographic variables. We have included the sighting data and some of the environmental data from that study here (less than 40% of our total data set) to examine cetacean habitat throughout the entire northern Gulf of Mexico with an expanded set of environmental variables and new statistical analyses. With regard to Risso's dolphin habitat, we have used the same sighting, depth, and depth gradient data presented in Baumgartner (1997). To these, we have added physical and biological oceanographic variables to test and extend the conclusions of Baumgartner (1997) and to strengthen the univariate and multivariate interspecies comparisons described below.

Analytical methods

The analysis of the sighting and effort data sets was conducted in two parts: 1) univariate and multivariate interspecies comparisons of the environmental variables measured at each cetacean sighting and 2) comparisons of each species' distribution with respect to the environmental variables to that of the effort. The former analysis examined the null hypothesis that each species had similar distributions with respect to each of the environmental variables. This was tested with Mood's median test (Conover, 1980) and the Kruskal-Wallis test (Sokal and Rohlf, 1981) as nonparametric substitutes for a one-way analysis of variance. Multivariate analysis of variance (MANOVA) and canonical linear discriminant function (LDF) analysis (Huberty, 1994; Johnson, 1998) with rank-transformed environmental variables were used to further examine interspecies differences. These analyses were conducted with the CANDISC procedure of the Statistical Analysis System (SAS, 1989), version 6.12. The MANOVA detects species group differences in multivariate space and

the canonical LDF analysis describes which environmental factors contribute most to these group differences. The canonical LDF analysis is accomplished by finding a linear combination of the environmental variables that best discriminates between the species groups. These linear combinations (canonical variables) are then examined by using the LDF structure correlations (Huberty, 1994) to assess their ecological meaning and significance. The structure correlations are essentially the correlations between the canonical variables and the original environmental variables and their interpretation is analogous to the interpretation of factor loadings in factor analysis.

The second analysis uses univariate and bivariate chi-squared (χ^2) tests, Mann-Whitney tests, Monte Carlo tests, and equal-effort sighting rate distribution plots to determine the specific relationships between the distribution of each species and each of the environmental variables. For the χ^2 analysis, the effort data were used to compute expected uniform distributions for each species with respect to the individual environmental variables. Classes were chosen such that each contained an equal amount of effort (Kendall and Stuart, 1967). This approach "normalized" the sighting rates by creating class sizes of equal sighting probability based on the effort and guaranteed that the analysis would not be distorted by classes with exceptionally low or high amounts of effort. For a complete description of the methods used to compute the uniform distribution, see Baumgartner (1997). The actual distributions were then compared with the predicted uniform distributions by using the χ^2 statistic. Equal-effort sighting rate distribution plots were constructed directly from the contingency tables used in the χ^2 analyses. In some cases, the sample size was lower than the minimum required for a conservative χ^2 test (n=25), therefore the species' and effort distributions were compared by using a Mann-Whitney test.

Of the five species examined here, each had a distribution with respect to depth that was significantly different from a uniform distribution. Further analyses with Monte Carlo (randomization) tests were conducted to determine if the distribution of a particular species with respect to the other environmental variables was an artifact of that species' distribution with depth. For example, consider a hypothetical species that is only found on the continental shelf. The continental shelf in the northern Gulf of Mexico is characterized by low depth gradients, whereas the continental slope has high depth gradients and the abyssal plains of the deep Gulf have low depth gradients. Because this species occurs on the continental shelf, it would have distributions with respect to both depth and depth gradient that were significantly different from a uniform distribution. However, this species' distribution with respect to depth gradient is merely an artifact of its distribution with respect to depth because of a correspondence between shallow depths and low depth gradients over the continental shelf.

The Monte Carlo tests consisted of randomly choosing n transect sections from the effort data set that had the same depth distribution as the n sightings of the species of interest. These transect sections represent n "virtual" cetacean sightings that have the same depth distribution as the species of interest but have a random distribution with respect to all of the other environmental variables. A χ^2 analysis was then conducted to determine if the distribution of the "virtual" sightings with respect to the particular environmental variable of interest (e.g. depth gradient in the example above) was different from a uniform distribution predicted by the effort. The process of choosing n "virtual" sightings and of conducting the χ^2 analysis was performed 10,000 times. The proportion of the resulting 10,000 χ^2 statistics that exceeded the χ^2 statistic associated with the species' actual distribution with respect to the environmental variable of interest was considered a P-value. This P-value represented the probability that the actual χ^2 statistic could have been observed by chance and was used to test the null hypothesis that the species' distribution with respect to the environmental variable of interest was the same as a uniform distribution given its distribution with respect to depth.

Results

NOAA Ship *Oregon II* completed 113 days of effort during the spring surveys from 1992 to 1994 and sampled the entire oceanic northern Gulf of Mexico once each year. A total of 9101 1-km transect sections (units of effort) were completed during adequate sighting conditions. The amount of environmental data available for each transect section was dependent on survey design, on instrument availability and performance, and, in the case of the remotely sensed sea surface temperature variability, on satellite orbital parameters and cloud conditions (Table 2).

The Loop Current penetrated into the eastern Gulf to at least 27.5°N during each of the surveys and warm-core eddies could usually be found in the central and western Gulf (Fargion et al.[10]). Both the Loop Current and the warm-core eddies were often accompanied by cold-core features at their peripheries. Examples of the major oceanographic features of the northern Gulf are shown in the composite AVHRR sea surface temperature image and the contoured depth of the 15°C isotherm (Fig. 2). The Loop Current is easily identifiable as the broad region in the eastern Gulf where the 15°C isotherm was at depths below 250 to 300 m and sea surface temperatures reached a local maximum. The remnants of a warm-core eddy (Eddy V) are evident in the northwestern Gulf centered at about 27.0°N, 95.5°W (Jockens et al., 1994; Fargion et al.[10]). Warm-core features like the Loop Current were characterized by depressed isotherms and were often accompanied by warm surface temperatures and low zooplankton biomass (Fig. 3). Surface temperature gradients were high at the edge of these mesoscale features when

[10] Fargion, G. S., L. N. May, T. D. Leming, and C. Schroeder. 1996. Oceanographic surveys. *In* Distribution and abundance of cetaceans in the north-central and western Gulf of Mexico: final report, vol.II: technical report (R.W. Davis and G.S. Fargion, eds.), p. 207–269. U.S. Department of the Interior, Minerals Management Service, OCS Study MMS 96-007. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

Table 2

Number of 1-km transect sections (units of effort) with valid data for each environmental variable.

Variable	1992	1993	1994	Total	
Depth	3454	2373	3274	9101	(100%)
Depth gradient	3454	2373	3274	9101	(100%)
Surface temperature	1414	2245	2915	6574	(72%)
Surface temperature standard deviation	688	1084	498	2270	(25%)
Depth of 15°C isotherm	2357	1939	2669	6965	(77%)
Surface chlorophyll concentration	2844	2277	2859	7980	(88%)
Zooplankton biomass	2127	1103	1419	4649	(51%)

Table 3

Correlation matrix of environmental variables. Correlation coefficients for surface chlorophyll and zooplankton biomass were computed from the station samples (not from the interpolated fields). SD = standard deviation.

Variable	Depth	Depth gradient	Surface temperature	Surface temperature SD	Depth of 15°C isotherm	Surface chlorophyll
Depth gradient	–0.003					
Surface temperature	0.104*	0.098*				
Surface temperature SD	–0.067*	0.032	0.019			
Depth of 15°C isotherm	0.297*	–0.139*	0.199*	0.365*		
Surface chlorophyll	–0.341*	0.013	–0.250*	–0.165	–0.166	
Zooplankton biomass	–0.224*	–0.064	–0.192	0.141	–0.380*	0.710*

* indicates $P < 0.05$.
* indicates $P < 0.01$.

their surface temperature signatures were strong.

Many of the environmental variables in the effort data set were significantly correlated with one another ($P<0.05$), but correlation coefficients were less than 0.3 in most cases (Table 3). The high correlation between surface chlorophyll and zooplankton biomass was strongly influenced by stations on the continental shelf where both surface chlorophyll and zooplankton biomass were typically quite high. The surface chlorophyll measurements collected on the shelf were significantly higher than those from oceanic waters (Mann-Whitney, $U=4.44$, $P<0.0001$), whereas the median zooplankton biomass measured on the shelf (10.1 cc/100 m^3) was almost twice as large as the median of the oceanic observations (5.4 cc/100 m^3). The correlation coefficient between the surface chlorophyll and zooplankton biomass measured in oceanic waters was not significantly different from zero ($P>0.05$). This contrast between the continental shelf and more oceanic waters was also manifested in the inverse relationships detected between depth and surface chlorophyll and between depth and zooplankton biomass.

Table 4

Number of group sightings (n), sighting rate (group sightings per 100 km) and mean, standard deviation (SD), minimum (Min) and maximum (Max) group size of the five most frequently encountered species or species groups.

Species	n	Sighting rate	Group size			
			Mean	SD	Min	Max
Bottlenose dolphin	89	0.98	14.7	22.7	1	150
Risso's dolphin	67	0.74	10.8	7.3	2	40
Kogia spp.	56	0.62	2.1	1.6	1	8
Pantropical spotted dolphin	107	1.18	51.8	42.4	3	180
Sperm whale	43	0.47	2.5	1.9	1	11

Of the 614 cetacean groups sighted between 1992 and 1994, the most frequently encountered species were the bottlenose dolphin, Risso's dolphin, *Kogia* spp., pantropical spotted dolphin, and sperm whale (Table 4). The *Ko-*

gia spp. group was made up of sightings of dwarf sperm whales (n=32), pygmy sperm whales (n=7), and those small whales that could only be identified to the genus *Kogia* (n=17). The spatial distributions of sightings suggest high use areas for each species (Fig. 4), but these are heavily influenced by the distribution of the sighting effort. To better capture the true spatial distributions, the location of each sighting and 1-km transect section was projected onto the 200-m isobath (by using the minimum distance to this isobath) and equal-effort sighting distributions were generated with respect to the distance along the 200-m isobath (Fig. 4). Chi-squared analyses indicated that all of the species' distributions, except the *Kogia* spp. group, were significantly different from a uniform distribution (P<0.01). The northwestern Gulf of Mexico (west of the Mississippi River Delta) had much lower group sighting rates of each cetacean species when compared with the northeastern Gulf (east of the Mississippi River Delta). To the south of New Orleans, the Mississippi Canyon and just seaward of the Mississippi River Delta were regions of high group encounter rates for bottlenose dolphins, Risso's dolphins, and sperm whales. Just to the east of this region and south of Mobile Bay, pantropical spotted dolphin sighting rates reached a local maximum. Along the steep upper continental slope of the Florida Escarpment between Tampa and Key West, very high relative abundances of Risso's dolphins, pantropical spotted dolphins, and sperm whales were observed.

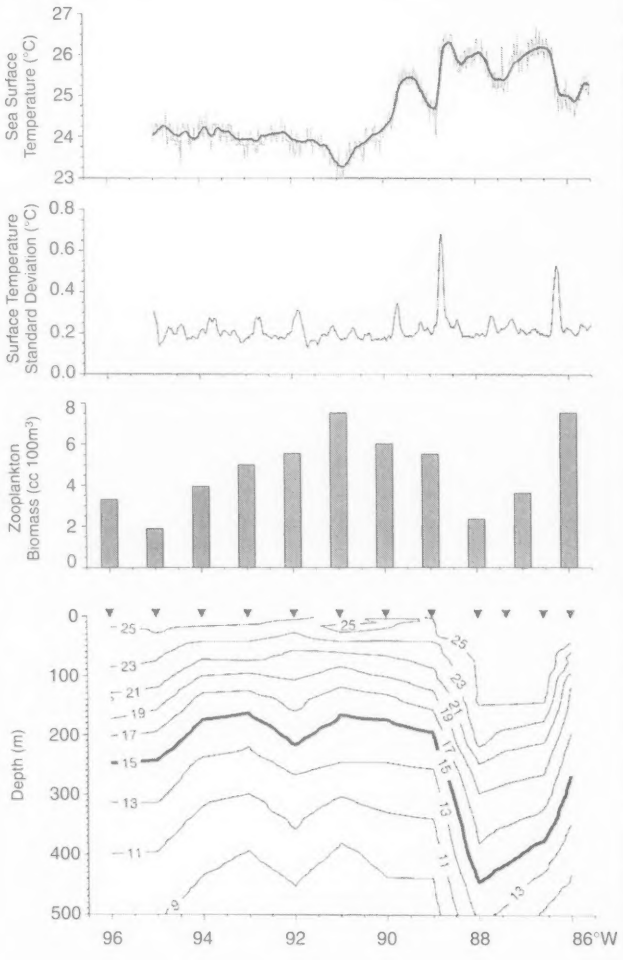

Figure 3

Surface temperature (raw temperatures in gray, 10 km radius average in black), surface temperature variability (standard deviation in 10 km radius), epipelagic zooplankton biomass and vertical temperature structure along 27°N observed between 19 May and 1 June 1993. Surface temperature and surface temperature variability were obtained from the composite satellite image shown in Figure 2. The inverted triangles indicate CTD/XBT station locations from which the temperature section was derived.

Examination of the mean, median, first and third quartiles, and standard deviation of the environmental variables for each species suggested significant interspecies differences (Fig. 5). The null hypothesis of equal medians for each species was rejected for depth, depth gradient, surface temperature, and zooplankton biomass (Mood's median test, P<0.01). Similarly, the null hypothesis of equal "locations" was rejected with a Kruskal-Wallis test for depth, depth gradient, zooplankton biomass (P<0.01), and surface temperature (P<0.05). The bottlenose dolphin had the lowest median depth, depth gradient, and surface temperature of all the species. The Risso's dolphin had the highest median depth gradient and surface temperature and the *Kogia* spp. had the highest median zooplankton biomass. The bottlenose dolphin's median habitat was so different from the others that if this species was removed from each of the Mood's median tests, the null hypothesis of equal medians between species would be rejected for only depth (P<0.01) and zooplankton biomass (P<0.05).

Despite clear heterogeneity of variances (Fig. 5A), a one-way analysis of variance indicated that the cetacean distributions with respect to depth were significantly different. Furthermore, a Duncan's multiple range test suggested species groupings by depth (P<0.05) that were qualitatively accurate and in agreement with earlier results (Mullin et al., 1994). These species groupings were 1) bottlenose dolphins, 2) Risso's dolphins and *Kogia* spp., and 3) pantropical spotted dolphins and sperm whales. Bottlenose dolphins were encountered predominantly over the continental shelf and were never sighted seaward of the 750-m isobath. Risso's dolphins and *Kogia* spp. were distributed mostly over the upper continental slope, whereas pantropical spotted dolphins

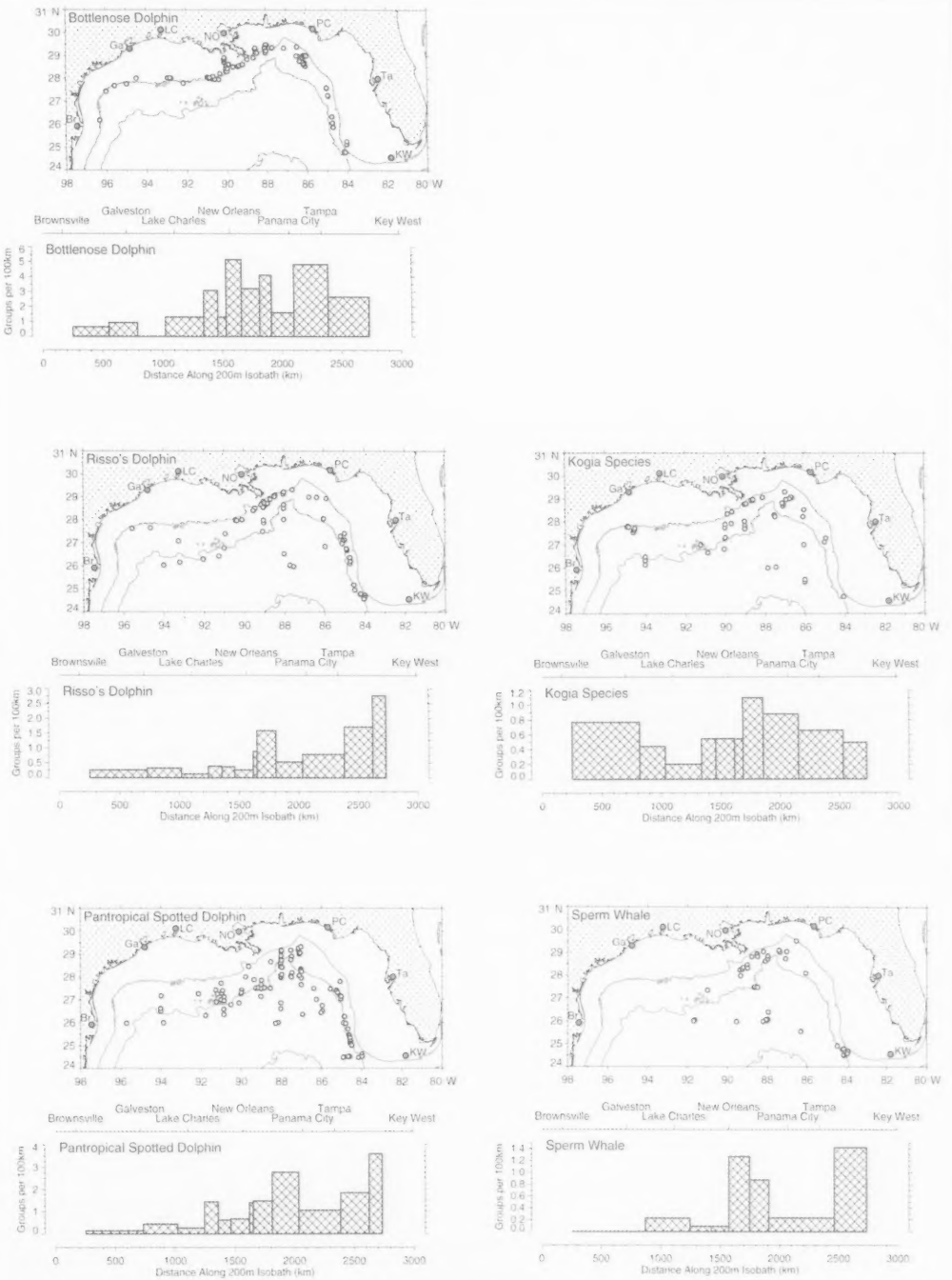

Figure 4

Spatial distribution of group sightings and sighting rates for each species. Sightings and 1-km transect sections (effort) were projected onto the 200-m isobath and the group sighting rate distributions were computed by using equal-effort class sizes. The sighting rate distribution of the bottlenose dolphin only includes effort from 1000 m depth and shallower because no bottlenose dolphins were encountered seaward of the 750-m isobath. The sighting maps and sighting rate distribution plots are aligned geographically to facilitate comparison. The 200- and 2000-m isobaths are shown in the sighting maps.

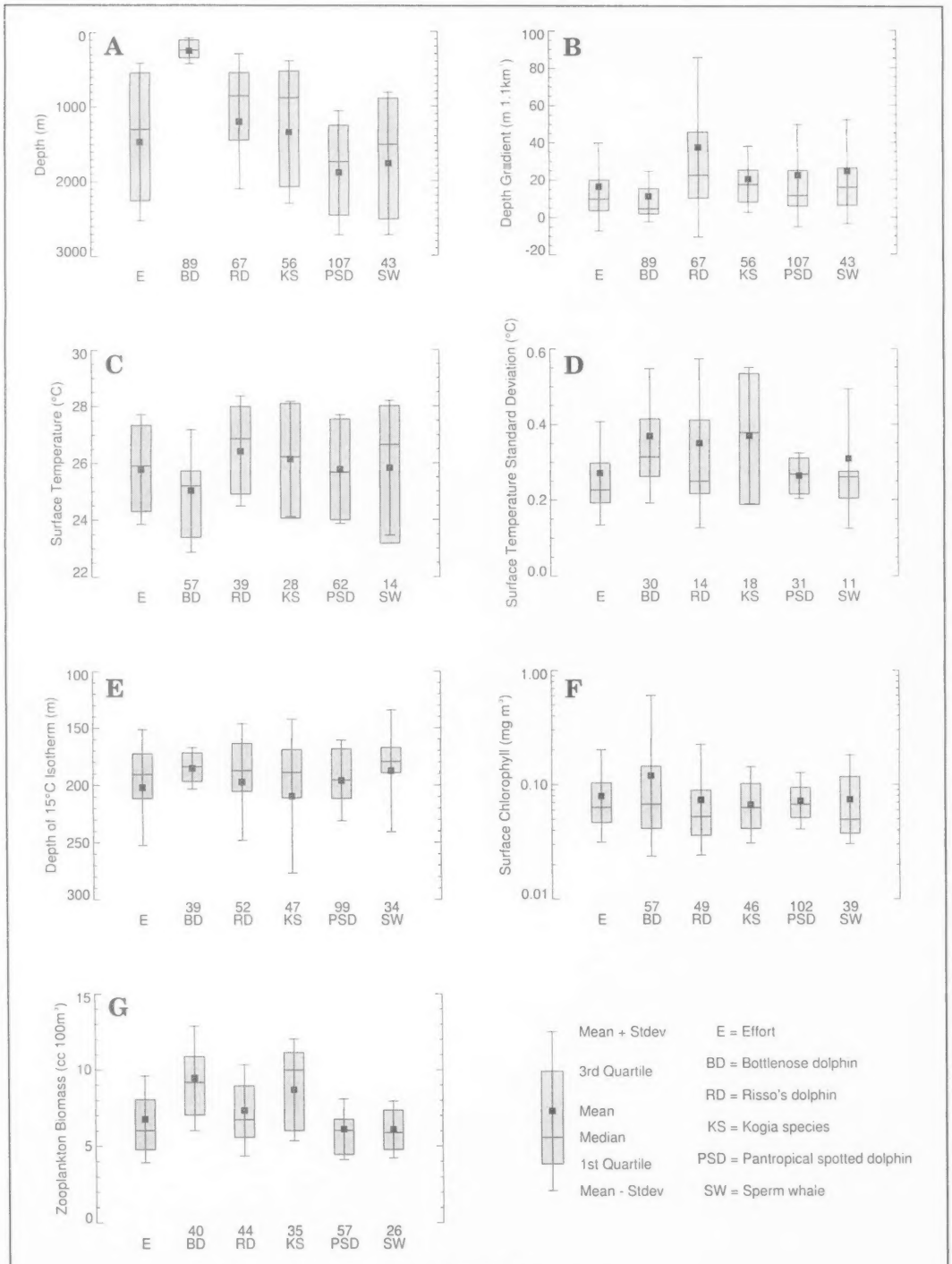

Figure 5

Mean, median, interquartile range, and standard deviation of (**A**) depth, (**B**) depth gradient, (**C**) surface temperature, (**D**) surface temperature variability, (**E**) depth of the 15°C isotherm, (**F**) surface chlorophyll, and (**G**) epipelagic zooplankton biomass for each species and the 1-km transect sections (effort). The sample size (n) is shown above each species abbreviation.

and sperm whales had distributions that extended from the upper continental slope to the deep Gulf. Mann-Whitney tests between Risso's dolphins and *Kogia* spp. for each of the environmental variables indicated that only their distributions with respect to depth gradient (U=2.12, P<0.05) and zooplankton biomass (U=1.69, P<0.05) were significantly different. Similar tests between pantropical spotted dolphins and sperm whales indicated that their distributions with respect to the depth of the 15°C isotherm (U=2.26, P<0.05) alone were significantly different.

Differences between species were also detected with MANOVA and canonical linear discriminant function analysis. Unfortunately, low sample size for both sea surface temperature and sea surface temperature variability precluded their use in the multivariate analyses. Of the remaining variables, the sample sizes for each species were as follows: bottlenose dolphins (n=18), Risso's dolphins (n=35), *Kogia* spp. (n=25), pantropical spotted dolphins (n=51), and sperm whales (n=19). The null hypothesis of equal mean vectors was rejected in the MANOVA (Wilks' λ=0.446, P<0.0001). The first two canonical variables in the canonical LDF analysis accounted for 94.5% of the total variability, and likelihood ratio tests indicated that only the first two canonical variables were significant (P<0.01 for each). The structure correlations indicated that low depths and high zooplankton biomass were associated with positive values of the first canonical variable, whereas shallow occurrences of the depth of the 15°C isotherm and low surface chlorophyll concentration were associated with positive values of the second canonical variable (Fig. 6A). The separation between groups along canonical axis 1 supports the importance of depth in habitat partitioning in the northern Gulf of Mexico. The significance of zooplankton biomass in this first canonical variable was due to the inclusion of the bottlenose dolphin in the analysis and the presence of high zooplankton biomass on the continental shelf. Note that the bottlenose dolphin was clearly separated from the other species along canonical axis 1 and the sperm whale was separated from the other species on both canonical axes.

Because inclusion of the bottlenose dolphin strongly influenced the results of the multivariate analysis, a second analysis was conducted for just the oceanic species. The null hypothesis of equal mean vectors was rejected

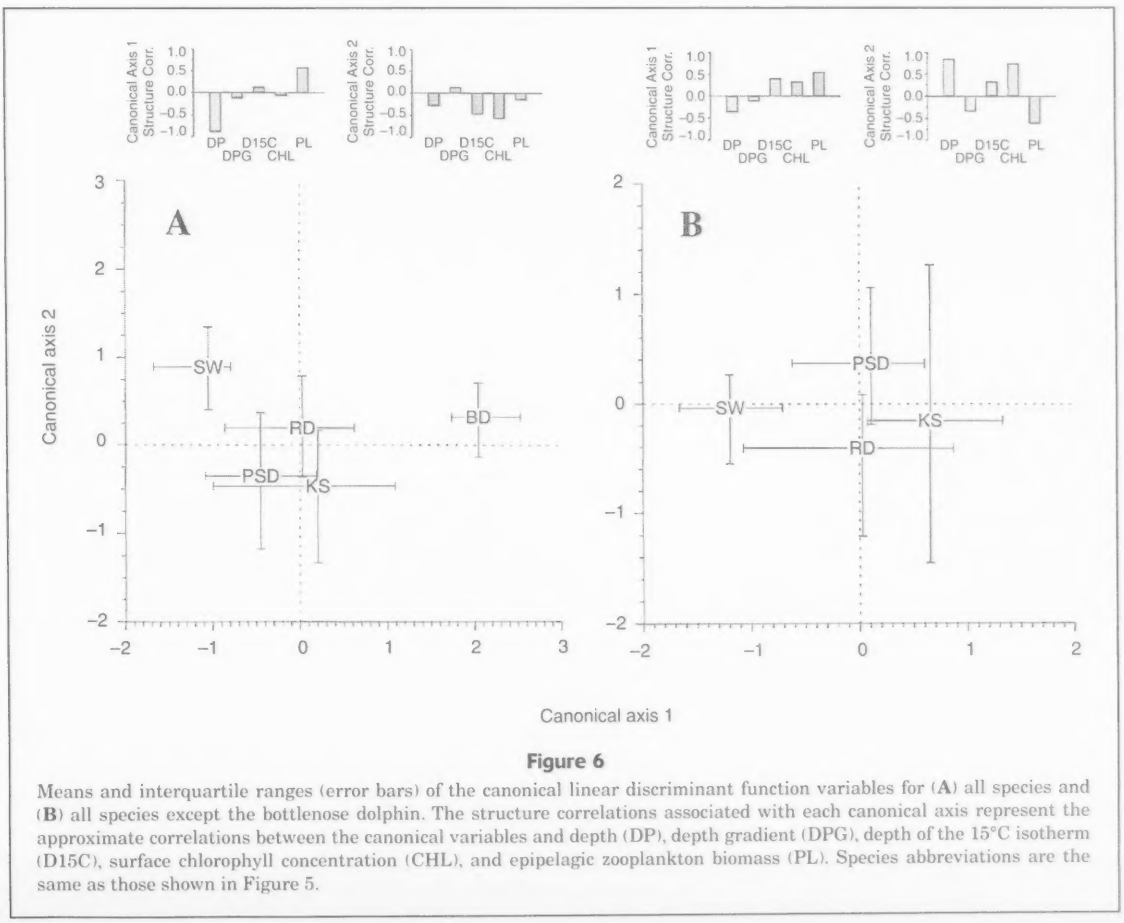

Figure 6

Means and interquartile ranges (error bars) of the canonical linear discriminant function variables for (**A**) all species and (**B**) all species except the bottlenose dolphin. The structure correlations associated with each canonical axis represent the approximate correlations between the canonical variables and depth (DP), depth gradient (DPG), depth of the 15°C isotherm (D15C), surface chlorophyll concentration (CHL), and epipelagic zooplankton biomass (PL). Species abbreviations are the same as those shown in Figure 5.

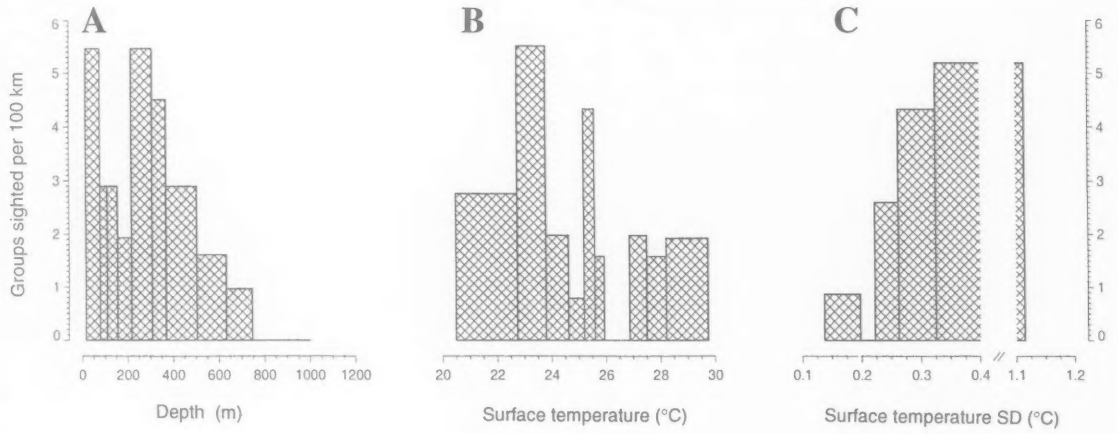

Figure 7

Sighting rate distributions of bottlenose dolphins with respect to (**A**) depth, (**B**) surface temperature and (**C**) surface temperature variability computed by using equal-effort class sizes.

again in the MANOVA (Wilks' λ=0.675, P<0.0001). The first two canonical variables in the canonical LDF analysis accounted for 94.2% of the total variability, and likelihood ratio tests indicated that only these first two canonical variables were significant (P<0.0001 for the first, P<0.05 for the second). The correlation structure suggested that high values of zooplankton biomass and deep occurrences of the depth of the 15°C isotherm were associated with positive values of the first canonical variable, whereas high values for depth and surface chlorophyll were associated with positive values of the second canonical variable (Fig. 6B). Although there seems to be considerable overlap between the Risso's dolphin, pantropical spotted dolphin, and *Kogia* spp. in the canonical space, the sperm whale is separated from the other species primarily along canonical axis 1 (Fig. 6B).

Bottlenose dolphin

Because the bottlenose dolphin was never encountered seaward of the 750-m isobath, only the surveyed transect sections shallower than 1000 m were used in the comparisons between the sightings and the effort. The distributions of this species with respect to depth, depth gradient, surface temperature, and surface temperature variability were significantly different from a uniform distribution (Table 5). Monte Carlo tests suggested that the distribution with respect to depth gradient may have been an artifact of the distribution with respect to depth (P>0.05; Table 5). The sighting rate distribution of the bottlenose dolphin with respect to depth (Fig. 7A) was bimodal as indicated by the peak in the sighting rate at the shallowest depth class (<75 m) and another peak just seaward of the shelf break. Although no coherent pattern was apparent in the sighting rate distribution with respect to surface temperature (Fig. 7B), group sighting rates increased with increasing surface temperature variability (Fig. 7C).

Interpretation of the sighting rate distributions for surface temperature and surface temperature variability was confounded by this species' bimodal distribution with respect to depth. To address this, the sightings were separated into a shelf group (<150 m) and a shelf break group (>150 m) by using the local minimum in the sighting rates with respect to depth as the separation criterion (Fig. 7A). The shelf dolphins (n=24) were found in cooler surface waters in relation to that observed during the sighting effort (Mann-Whitney test, U=2.23, P<0.05), whereas the distribution of the shelf break dolphins (n=33) with respect to surface temperature was not significantly different from the effort (Mann-Whitney test, U=1.03, P>0.05; χ^2 test, χ^2=9.7, df=5, P>0.05). Both the shelf (n=16, U=3.23, P<0.01) and shelf break bottlenose dolphins (n=14, U=2.93, P<0.01) were encountered in regions of significantly higher surface temperature variability in relation to the effort.

It should be noted that the bottlenose dolphin appears to have a distribution with respect to zooplankton biomass that is significantly different from the effort for all depths (Fig. 5G). In fact, a Mann-Whitney test supports this assertion (U=5.42, P<0.0001). Once the analysis is restricted to the continental shelf and upper continental slope (0–1000 m), however, the distribution of the bottlenose dolphin with respect to zooplankton biomass is not significantly different from the effort (U=0.19, P>0.05). This apparent discrepancy is due to higher zooplankton biomass over the continental shelf than anywhere else in the northern Gulf of Mexico.

Risso's dolphin

The distribution of the Risso's dolphin was significantly different from a uniform distribution for both depth and depth gradient (Table 5) and there was strong evidence

Table 5

Results for univariate χ^2, Mann-Whitney, and Monte Carlo tests. Values of 0.0000 for P indicate $P < 0.0001$.

		χ^2 test			Mann-Whitney		Monte Carlo
	n	χ^2	df	P	U	P	P
Bottlenose dolphin							
Depth	89	57.6	11	0.0000*			—
Depth gradient	89	23.1	11	0.0174			0.7474
Surface temperature	57	26.8	9	0.0015*			0.0224
Surface temperature standard deviation	30	17.3	4	0.0017*			0.0018*
Depth of 15°C isotherm	39	6.0	6	0.4184			0.4909
Surface chlorophyll	57	12.2	9	0.1999			0.4095
Zooplankton biomass	40	1.9	6	0.9268			0.9720
Risso's dolphin							
Depth	67	53.9	12	0.0000*			—
Depth gradient	67	57.4	12	0.0000*			0.0000*
Surface temperature	39	9.9	6	0.1296			0.1527
Surface temperature standard deviation	14				1.69	0.0456	
Depth of 15°C isotherm	52	16.3	9	0.0603			0.0971
Surface chlorophyll	49	9.2	8	0.3232			0.3227
Zooplankton biomass	44	7.3	7	0.3970			0.7056
Kogia spp.							
Depth	56	42.6	9	0.0000*			—
Depth gradient	56	20.4	9	0.0155			0.0690
Surface temperature	28	4.8	4	0.3038			0.3540
Surface temperature standard deviation	18				1.98	0.0238	
Depth of 15°C isotherm	47	7.2	8	0.5125			0.5371
Surface chlorophyll	46	3.4	7	0.8441			0.8560
Zooplankton biomass	35	31.6	5	0.0000*			0.0014*
Pantropical spotted dolphin							
Depth	107	50.6	11	0.0000*			—
Depth gradient	107	25.1	11	0.0088*			0.0687
Surface temperature	62	13.5	11	0.2614			0.3616
Surface temperature standard deviation	31	7.5	4	0.1096			0.1148
Depth of 15°C isotherm	99	19.1	11	0.0593			0.0748
Surface chlorophyll	102	20.6	11	0.0380			0.0985
Zooplankton biomass	57	16.4	9	0.0588			0.3522
Sperm whale							
Depth	43	14.5	7	0.0431			—
Depth gradient	43	13.7	7	0.0566			0.0965
Surface temperature	14				0.27	0.3921	
Surface temperature standard deviation	11				1.14	0.1268	
Depth of 15°C isotherm	34	11.0	5	0.0508			0.0388*
Surface chlorophyll	39	11.5	6	0.0741			0.0749
Zooplankton biomass	26	3.5	4	0.4729			0.7053

* indicates $P < 0.05$.
** indicates $P < 0.01$.

that the distribution with respect to depth gradient was not an artifact of the depth distribution ($P<0.0001$). The distribution with respect to surface temperature variability was significantly different from the effort ($P<0.05$; Table 5) and surface temperature variability at Risso's dolphin sightings was generally higher than the effort (Fig. 5D). The sighting rate distribution with respect to depth was modal about the upper continental slope (Fig. 8A), whereas group sighting rates increased with increasing depth gradient (Fig. 8B).

Kogia spp.

The distributions of the *Kogia* spp. with respect to depth, depth gradient, and epipelagic zooplankton biomass were significantly different from a uniform distribution (Table 5); however, the distribution with respect to depth gradient may have been an artifact of the depth distribution ($P>0.05$; Table 5). The distribution with respect to surface temperature variability was significantly different from the effort ($P<0.05$; Table 5), and the median value of surface temperature variability for *Kogia* spp. was the highest of all the species examined (Fig. 5D). *Kogia* spp. had a modal distribution about the upper continental slope (Fig. 9A) and group sighting rates increased with increasing zooplankton biomass (Fig. 9B). A bivariate χ^2 analysis (after Baumgartner, 1997) indicated that the distribution of *Kogia* spp. was significantly different from a uniform distribution with respect to both depth and zooplankton biomass ($\chi^2=29.2$, df=4, $P<0.0001$) and that in waters of high zooplankton biomass over the upper continental slope, group sighting rates were 2.5 times the average.

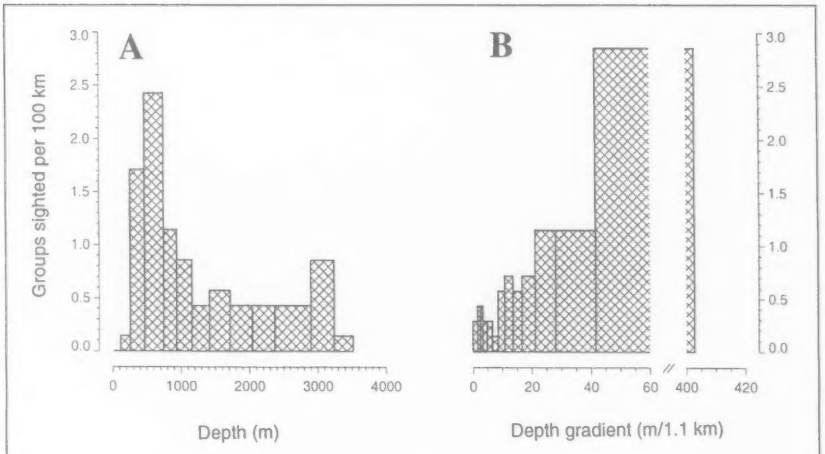

Figure 8

Sighting rate distributions of Risso's dolphins with respect to (**A**) depth and (**B**) depth gradient.

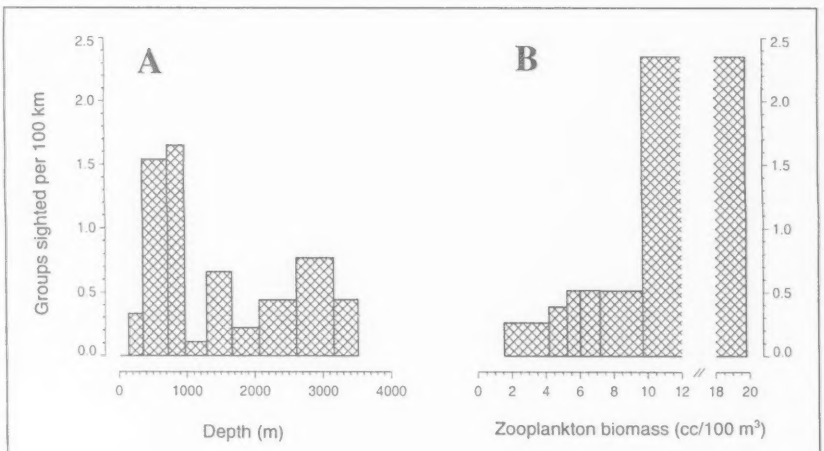

Figure 9

Sighting rate distributions of *Kogia* spp. with respect to (**A**) depth and (**B**) epipelagic zooplankton biomass.

Pantropical spotted dolphin

The distribution of the pantropical spotted dolphin was significantly different from a uniform distribution of depth, depth gradient, and surface chlorophyll (Table 5); however, the distributions with respect to depth gradient and surface chlorophyll may have been an artifact of the depth distribution ($P>0.05$; Table 5). This species was encountered only once near the shelf break (Fig. 10) and if the χ^2 analysis was limited to sightings and effort deeper than 500 m, then the depth distribution would not be significantly different from a uniform distribution ($\chi^2=14.5$, df=11, $P>0.05$).

Sperm whale

The distribution of the sperm whale with respect to depth was significantly different from a uniform distribution (Table 5; Fig. 11A). Only one group of sperm whales was encountered near the shelf break and if the χ^2 analysis was limited to sightings and effort deeper than 500 m, then the depth distribution would not be significantly different from a uniform distribution ($\chi^2=2.2$, df=7, $P>0.05$). There is evidence to suggest that the distribution with respect to the depth of the 15°C isotherm was significantly different from a uniform distribution when the depth distribution is taken into consideration (Monte Carlo test, $P<0.05$; Table 5). In waters where the 15°C isotherm was deeper than 200 m, the group sighting rate of sperm

whales was less than a quarter of the average and was one-sixth the sighting rate in waters where the depth of the 15°C isotherm was shallower than 200 m (Fig. 11B)

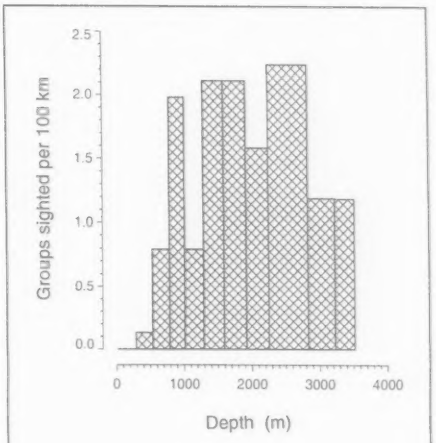

Figure 10

Sighting rate distribution of pantropical spotted dolphins with respect to depth.

Discussion

Previous studies have indicated that cetacean habitat within several hundred kilometers of the coast is most effectively partitioned by depth (Davis et al., 1998; CETAP[5]; Dohl et al[6].; Dohl et al.[7]; Green et al.[8]; Davis et al.[11]). In the northern Gulf of Mexico, each of the five species examined in our study could be distinguished from at least three of the others by its distribution with depth alone. Although the distributions of Risso's dolphin and the *Kogia* spp. with respect to depth overlapped on the upper continental slope, their distributions over the upper slope could be distinguished by using depth gradient and zooplankton biomass. The distributions of pantropical spotted dolphins and sperm whales with respect to depth were very similar over the continental slope and deep Gulf, but their distributions differed with respect to the depth of the 15°C isotherm. These results suggest that cetaceans partition the northern Gulf of Mexico according to each species' habitat preferences which are presumably based on different prey distributions. It is important to note that this partitioning does not necessarily imply spatial separation. Given the right conditions (e.g. waters 500–750 m deep over a steep section of the continental slope with high zooplankton biomass in the upper 200 m), many of these cetaceans could be encountered in the same area. Some of the environmental variables that are important descriptors of cetacean habitat (e.g. zooplankton biomass, depth of the 15°C isotherm, and surface temperature variability) vary over time, and therefore the locations and spatial extent of each species' habitat may vary over time as well.

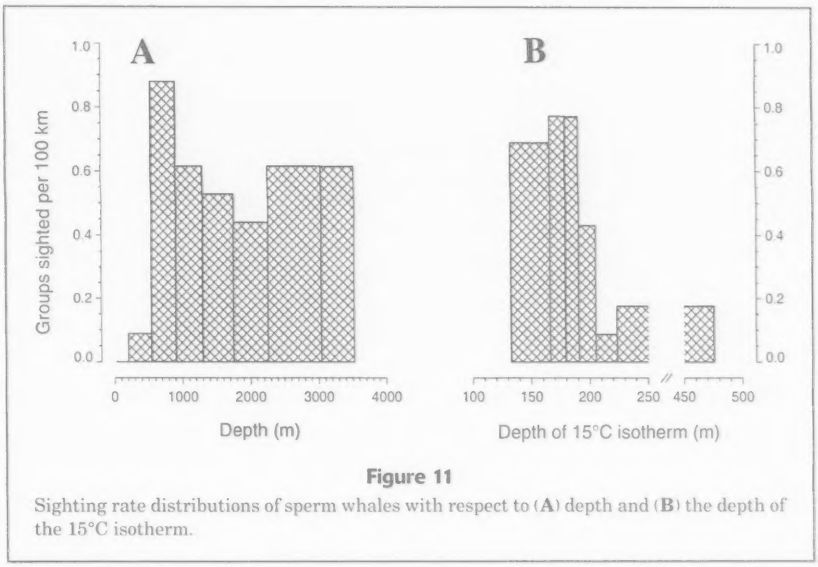

Figure 11

Sighting rate distributions of sperm whales with respect to (**A**) depth and (**B**) the depth of the 15°C isotherm.

Two regions of the northern Gulf of Mexico seem to be particularly important habitats for some of the more frequently encountered species during the spring (Fig. 4): the vicinity of the Mississippi River plume and just seaward of the southwestern Florida continental shelf. The Mississippi River injects nutrients into an otherwise oligotrophic oceanic Gulf in a region where the continental shelf is very narrow and the upper continental slope is quite steep. The rate of primary productivity and the standing stocks of chlorophyll and plankton associated with the nutrient-rich, fresh-water plume are high in relation to other regions in the oceanic Gulf (El-Sayed, 1972; Dagg et al., 1988; Ortner et al., 1989; Müller-Karger et al., 1991). Consequently, the plume region may provide feeding oppor-

[11] Davis, R. W., G. S. Fargion, W. E. Evans, L. N. May and T. D. Leming. 1996. Cetacean habitat. *In* Distribution and abundance of cetaceans in the north-central and western Gulf of Mexico: final report, vol. II: technical report (R. W. Davis and G. S. Fargion, eds.), p. 329–349. U.S. Department of the Interior, Minerals Management Service, OCS Study MMS 96-007. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

tunities for cetaceans through local trophic interactions. Likewise, the area west of the southwestern Florida shelf break may be another region of high productivity. The physical oceanography of this region is characterized by the formation of a cyclonic meander or eddy in the spring between the Loop Current to the west and the steep Florida Escarpment to the east (Cochrane, 1972; Vukovich et al., 1979; Vukovich and Maul, 1985). Maul et al. (1984) observed that bluefin tuna catch per unit of effort inside a cold-core meander in this region was three times higher than in the central Gulf the previous year. Between 83–86°W and 24– 27°N in oceanic waters, the sighting rates of Risso's dolphins, pantropical spotted dolphins, and sperm whales were 3.8, 2.6, and 2.8 times higher than the average sighting rate and 4.9, 3.0, and 3.3 times higher than the sighting rate outside of this region, respectively.

Bottlenose dolphin

The bottlenose dolphin's distribution in the northern Gulf of Mexico is markedly different from the other species examined in our study. This species and the Atlantic spotted dolphin are the only cetaceans that are routinely encountered on the continental shelf (Fritts et al., 1983; Mullin et al., 1994; Jefferson and Schiro, 1997; Hansen et al.[3]). Caution is warranted when interpreting the bimodal distribution of bottlenose dolphin sighting rates with respect to depth (Fig. 7A). Effort on the continental shelf was neither extensive nor distributed uniformly throughout the northern Gulf. During the CETAP study (Kenney, 1990; CETAP[5]), a distinct bimodal distribution of bottlenose dolphins was observed north of Cape Hatteras. Bottlenose dolphins were concentrated during warm months in waters less than 25 m and year round near the 1000-m isobath and some groups were sighted in waters as deep as 4712 m (CETAP[5]). This bimodal distribution is suggestive of the inshore (coastal) and offshore forms of bottlenose dolphins described by others (Norris and Prescott, 1961; Walker, 1975; Leatherwood and Reeves, 1982; Shane et al., 1986; Kenney, 1990; Walker[12]) and supported by mitochondrial DNA (Dowling and Brown, 1993; Curry and Smith, 1997), hematological (Duffield et al., 1983; Hersh and Duffield, 1990), and morphological (Hersh and Duffield, 1990) evidence. The spatial distribution of bottlenose dolphin group sightings from aerial surveys on the continental shelf of the Gulf of Mexico (Blaylock et al., 1995) and off the southeast U.S. coast south of Cape Hatteras (Blaylock and Hoggard, 1994), however, was not characterized by any large-scale discontinuities in bottlenose dolphin distribution similar to those observed north of Cape Hatteras.

The shelf bottlenose dolphins were found in regions with cooler than expected surface waters and high surface temperature variability. These oceanographic characteristics are consistent with the cool and fresh water side of fronts associated with river plumes and, indeed, sighting rates of the shelf bottlenose dolphins were particularly high near the Mississippi River Delta. Sighting rates of the shelf break bottlenose dolphins were more evenly distributed in the central and eastern Gulf and the high surface temperature variability observed near these dolphins suggests a potential association with shelf break fronts.

Risso's dolphin

Baumgartner (1997) examined the same 1992–94 spring cruise data used in our study with the intent of defining Risso's dolphin habitat in terms of the physiography of the northern Gulf of Mexico. Using both univariate and bivariate analyses, he determined that the sighting rate of Risso's dolphin groups between the 350- and 975-m isobaths and in depth gradients exceeding 24 m per 1.1 km was nearly 5 times the average. Of the groups encountered outside this region, 40% were sighted within 5 km of it. Aerial survey data collected during all seasons between 1992 and 1994 were used to independently assess this habitat model. Sighting rates from these surveys were nearly 6 times the average inside this core habitat, and of the groups encountered outside of this region, 73% were sighted within 5 km of it.

The distribution of Risso's dolphin along the continental slope has been noted in several studies (Würtz et al., 1992; CETAP[5]; Dohl et al.[6]; Dohl et al.[7]; Green et al.[8]; Davis et al.[11]) and some evidence exists to support this species' association with the steeper sections of the upper continental slope elsewhere. Off the Oregon and Washington coasts, Green et al.[8] observed that Risso's dolphin encounter rates over the continental slope (200–2000 m) were seven times greater than on the shelf and that the groups sighted on the shelf were very close to the shelf break. Compared with the northern Gulf of Mexico, almost the entire Oregon–Washington continental slope can be considered steep with depth gradients in excess of 22 m per 1.1 km (Fig. 11 in Green et al.[8]). Dohl et al.[7] found a similar distribution off central and northern California, where the majority of Risso's dolphin sightings were between the 183- and 1830-m (100–1000 fathom) isobaths. As is the case off Oregon and Washington, virtually all of the continental slope off central and northern California can be considered very steep (Fig. 1 in Dohl et al.[7]). The physiography of the northwestern Atlantic Ocean is much more like that found in the northern Gulf of Mexico and the CETAP study (Hain et al., 1985; Kenney and Winn, 1986; CETAP[5]) found Risso's dolphins concentrated at the shelf break (mode of 478 sightings was 183 m depth) and distributed over the entire continental slope (average of 478 sightings was 1092 m).

Baumgartner (1997) hypothesized that Risso's dolphins aggregate along the upper continental slope because of the presence of a persistent ocean front separating the relatively cool and fresh waters of the continental shelf and the more warm and salty waters of the oceanic Gulf. This shelf break front may provide greater feeding opportuni-

[12] Walker, W. A. 1981. Geographical variation in morphology and biology of bottlenose dolphins (*Tursiops*) in the eastern North Pacific. Southwest Fisheries Center Administrative Report LJ-81-03C, 52 p. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.]

ties because of enhanced local productivity or because it forms a border between two separate, exploitable ecosystems. The observations of higher than expected surface temperature variability at Risso's dolphin sightings seem to support this hypothesis, but the evidence is rather tenuous given the small sample size (n=14).

Kogia spp.

Kogia spp. were predominantly encountered along the upper continental slope in regions with high epipelagic zooplankton biomass. Their distribution with respect to depth in the northern Gulf of Mexico is in agreement with inferences drawn from a stomach content study of stranded *Kogia* spp. in South Africa where cephalopods typical of the continental slope were identified as the largest constituent of the stranded whales' stomach contents.[13] Further stomach content and stable isotope analyses suggest that pygmy and dwarf sperm whales consume different prey species and therefore may occupy different habitats.[14,15] No such separation was detectable in our study because of the low sample size for the individual species and the difficulty of positively identifying each at sea. Some diet overlap was observed between the two species off South Africa[14] and therefore the association between *Kogia* spp. and high epipelagic zooplankton biomass in the northern Gulf of Mexico may be due to the utilization of zooplankton in the diet of one or more of their common prey species.

Of all the cetaceans, *Kogia* spp. had the highest median value for surface temperature variability which suggests a similar association with ocean fronts as that observed for Risso's dolphins. Sample size for this variable was unfortunately low (n=18) however; therefore it is difficult to accurately describe this potential association. Because the upper continental slope can be a region of persistent frontal activity, it is conceivable that the distribution of both Risso's dolphins and *Kogia* spp. with respect to surface temperature variability may have been a consequence of their distribution with depth. The low sample sizes for each of these species precludes any analysis that may have been able to further support or refute these hypotheses.

Pantropical spotted dolphin

The distribution of the pantropical spotted dolphin was not significantly different from a uniform distribution with respect to any of the environmental variables, except depth. Pantropical spotted dolphins are rarely encountered on the continental shelf in the northern Gulf of Mexico (Jefferson and Schiro, 1997) and from the results obtained in our study, are probably evenly distributed with depth over the continental slope and deep Gulf. These results were surprising in light of this species' spatial distribution in the northern Gulf of Mexico (Fig. 4). Local maxima in group encounter rates occurred southwest of Panama City and along the Florida Escarpment northwest of Key West. The coherent pattern in Figure 4 strongly suggests the existence of high-use areas for this species, but the characteristics that make these regions attractive to pantropical spotted dolphins were not observed in the chosen set of environmental variables used in our study. Davis et al.[16] reported that oceanic stenellids (pantropical spotted dolphins, striped dolphins [*Stenella coeruleoalba*], spinner dolphins [*Stenella longirostris*], and Clymene dolphins [*Stenella clymene*]) were more frequently encountered in cyclonic, cold-core eddies and less frequently encountered in anticyclonic, warm-core eddies than expected based on the distribution of the GulfCet program sighting effort in the northern Gulf of Mexico. Although no such relationship was detected in our study, species grouping, confounding by other environmental or behavioral factors or temporal variability in habitat associations (or both) or prey availability could easily account for the apparent discrepancy between these two studies.

Sperm whale

Like the pantropical spotted dolphin, the sperm whale was never encountered on the continental shelf and appears to have a roughly even distribution with respect to depth over the continental slope and deep Gulf. The distributions of these two species with respect to the depth of the 15°C isotherm were significantly different, however, and the canonical LDF analysis suggested that this variable contributed to the separation between sperm whales and the other oceanic cetaceans (Fig. 6B). Sperm whales were encountered much less frequently in regions where the depth of the 15°C isotherm was quite deep (Fig. 11B), which suggests that this species avoids the interior of anticyclonic, warm-core features such as the Loop Current or warm-core mesoscale eddies. Waring et al. (1993) and Griffin (1999) described similar results from studies of sperm whale distributions in and around the periphery of warm-core eddies associated with the Gulf Stream in the northwest Atlantic Ocean. Davis et al.[16] and Biggs et al. (2000) reported that sperm whales were not only encountered outside of anticylonic features in the northeastern Gulf of Mexico, but most of the visual and acoustic contacts with

[13] Klages, N. 2000. Personal commun. Port Elizabeth Museum at Bayworld, P.O. Box 13147, Humewood 6013, South Africa.

[14] Plön, S. 2000. Personal commun. School of Biological Sciences, Thomas Building, Level 2, Univ. Auckland, Private Bag 92019, Auckland, New Zealand.

[15] Barros, N. 2000. Personal commun. Center for Marine Mammal and Sea Turtle Research, Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL 34236-1096.

[16] Davis, R. W., J. G. Ortega-Ortiz, C. A. Ribic, W. E. Evans, D. C. Biggs, P. H. Ressler, J. H. Wormuth, R. R. Leben, K. D. Mullin, and B. Würsig. 2000. Cetacean habitat in the northern Gulf of Mexico. *In* Cetaceans, sea turtles and seabirds in the northern Gulf of Mexico: distribution, abundance and habitat associations, vol. II: technical report (R. W. Davis, W. E. Evans, and B. Würsig, eds.), p. 217–253. U.S. Department of the Interior, Geological Survey, Biological Resources Division, USGS/BRD/CR-1999-0006 and Minerals Management Service, OCS Study MMS 2000-003. [Available from Public Information Office, MS 5034, Gulf of Mexico Region, Minerals Management Service, 1201 Elmwood Park Blvd., New Orleans, LA 70123-2394.]

sperm whales during the GulfCet II focal cruises were in regions characterized by cyclonic mesoscale features.

Jaquet (1996) reviewed a variety of sperm whale habitat studies that seemed to have contradictory conclusions regarding the primary oceanographic processes influencing sperm whale distribution (namely upwelling and downwelling). Jaquet attributed these discrepancies to a problem of defining the appropriate spatial and temporal scales, and she and others illustrated this point by demonstrating a varying but positive correlation between historical sperm whale catches and surface chlorophyll over increasing temporal and spatial scales in the equatorial Pacific (Jaquet et al., 1996). These results seem to indicate that upwelling, which contributes to increased surface phytoplankton biomass, is a predominant factor in influencing sperm whale distribution in the equatorial Pacific. Historical catches in temperate waters, however, are not at all correlated with surface chlorophyll (see Fig. 1 of Jaquet, 1996 and Fig. 1 of Jaquet et al., 1996) which suggests that other oceanographic processes or physiographic influences may be important (e.g. downwelling or biological-physical processes associated with continental slopes). At comparatively short time scales and small spatial scales, we found no evidence to suggest a relationship between the distribution of sperm whales and surface chlorophyll in the northern Gulf of Mexico. Even at longer temporal and larger spatial scales, we would expect this same result because the oceanic Gulf is persistently oligotrophic both in time and space (Müller-Karger et al., 1991; Longhurst, 1998).

Berzin (1971) examined harvest records from the worldwide sperm whale fishery and suggested that sperm whale distribution was closely linked to processes that supported the meso- and bathypelagic food webs. Because sperm whales feed almost exclusively on mesopelagic or demersal cephalopods (Clarke, 1986, 1996), they probably aggregate in areas where these prey are abundant. These deep-water prey species are entirely dependent on the rain of organic matter from the surface for their sustenance and so these species will be found in regions where the export of detritus from the surface is enhanced. This process occurs in convergence zones where downwelling forces surface biomass and oxygen into the deep ocean, such as in the middle of anticyclonic eddies, at the peripheries of cyclonic eddies, to the right (left) of surface ocean currents in the northern (southern) hemisphere, in the middle of the large-scale anticyclonic ocean gyres (e.g. the Sargasso Sea), or along fronts where surface water masses abut. The global sperm whale distribution maps provided by Townsend (1935) and Berzin (1971) do indeed suggest that this species was frequently harvested in or near large-scale oceanic convergence zones, especially along the subtropical convergence zones and the Antarctic polar front.

The distribution of sperm whales in the northern Gulf of Mexico and northwestern Atlantic Ocean (Waring et al., 1993; Griffin, 1999) seems contradictory to Berzin's hypothesis, however. Features such as the Loop Current or warm-core eddies rotate anticyclonically and have convergent centers in which downwelling occurs. According to Berzin's hypothesis, the interior of these features would be favorable to sperm whales because of the enhanced export of surface biomass to the deep ocean and the resultant increase in prey species. The interior of anticyclonic eddies in the northern Gulf of Mexico are, however, low in surface zooplankton biomass (Biggs, 1992). Although the rate of detrital export to the deep is enhanced by increased vertical velocities within these features, the amount of biomass actually exported may be too small to support large populations of deep-water prey.

Another possible explanation for the distribution of sperm whales with respect to the depth of the 15°C isotherm is related to the availability of prey. Berzin (1971) characterized cephalopods as thermophilic and thus indicated that they are distributed within a narrow range of ocean temperatures according to their species-specific thermal requirements or to the thermal requirements of their prey. These requirements not only govern the horizontal distribution of cephalopods, but their vertical distribution as well. Because warm-core features are characterized by depressed isotherms (e.g. Fig. 3), cephalopods within these features may be hundreds of meters deeper in the water column than in the waters outside these features. Despite their well-known ability to dive to great depths, foraging continuously at greater depths under warm-core features would be much more energetically expensive than foraging outside these features. Thus, when prey abundance inside and outside of warm-core eddies are equivalent, sperm whales may feed on prey distributed at shallower depths outside of these features to reduce their energy expenditure.

Caveats

It is important to remember that this study was limited to surveys conducted during the spring season. The spatial distribution of cetaceans may be different in other seasons because the oceanographic conditions of the northern Gulf of Mexico change over the course of the year. The northward penetration of the Loop Current into the Gulf varies on a quasi-annual basis (Vukovich et al., 1979; Sturges and Evans, 1983; Vukovich, 1995) and the variability in the position of the Loop Current affects the generation and positions of both anticyclonic and cyclonic eddies. This variability may, in turn, greatly influence the productivity and availability of prey species in the eastern Gulf of Mexico. In the northwestern Gulf, the slow march of warm-core eddies from east to west toward the "eddy graveyard" over the continental slope also varies with time and may affect the seasonal distribution of cetaceans. Hansen et al.[3] observed seasonal differences in cetacean abundance in the western and central regions of the northern Gulf of Mexico that may have been influenced by temporal changes in the local oceanography.

Another potential limitation of our study was the rather coarse environmental sampling. Although the CTD/XBT sampling strategy was sufficient to identify the large-scale oceanographic features, some of the most biologically significant processes in the oceanic Gulf of Mexico occur on smaller spatial scales. In particular, the outer edge of the Loop Current is frequently a site of upwelling and these divergent features often develop into cyclonic meanders

and eddies at the northern and eastern sides of the Loop Current (Vukovich and Maul, 1985). These cyclonic features are usually much smaller than the Loop Current itself or the warm-core features of the central and western Gulf (Cochrane, 1972). Along the latitude of 27°N and within 40 km of the Loop Current (near 88.8°W) in late spring, 1993, for instance, the satellite-borne AVHRR detected surface temperatures 1.5°C cooler than the Loop Current itself, but the vertical temperature structure, surface chlorophyll and zooplankton biomass associated with this narrow feature were not captured because of the coarse sampling strategy (Figs. 2 and 3). The recent GulfCet II program (Davis et al.[16]) examined cetacean habitat associations in the vicinity of cyclonic-anticyclonic eddy pairs in the northeastern Gulf of Mexico and demonstrated that these mesoscale hydrographic features can indeed influence cetacean distribution. In addition to the cyclonic features associated with the Loop Current, the CTD and XBT sampling strategy of our study did not resolve other potentially productive features that occur on smaller spatial scales, such as nutrient-rich Mississippi River plume waters entrained at the edge of the Loop Current (Maul, 1977; Müller-Karger et al., 1991) and shelf break fronts.

Future studies of cetacean habitats in the Gulf of Mexico should continue to consider these smaller scale features as potential sites of large cetacean aggregations because of their high levels of biological activity. These features could potentially 1) have high rates of primary productivity that is converted into prey biomass over short temporal and spatial scales, 2) concentrate prey through solely physical mechanisms or through physical-biological interactions or 3) make local prey more accessible to surface-bound cetaceans. Although investigating these processes is undoubtedly a challenge, it is important to elucidate what processes affect cetacean distribution and at what spatial and temporal scales these processes operate if we are to understand how oceanographic conditions affect cetacean ecology.

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Abstract—The Sea Turtle Stranding and Salvage Network, coordinated by the National Marine Fisheries Service through a network of state coordinators, archives data on sea turtles that strand along the U.S. coast. We conducted length-frequency analyses, using MULTIFAN software, to generate somatic growth functions for loggerhead sea turtles, *Caretta caretta*, that stranded along the Atlantic coast of Florida (n=1234) and along the U.S. coast of the Gulf of Mexico (n=570) between 1988 and 1995. In both regions, the size range of loggerhead sea turtles between the size at which they begin to recruit in substantial numbers from pelagic to neritic habitats (46 cm curved carapace length [CCL]) and minimum size at sexual maturity (87 cm CCL) was composed of 20 year classes and had similar von Bertalanffy growth functions. Our estimates of 20 year classes fall within the range of estimates calculated from previous studies (9 to 29 years) for this life stage. Because survivorship in this size range has been identified as critical for population recovery, an accurate estimate of life stage is essential for developing effective management plans.

Somatic growth function for immature loggerhead sea turtles, *Caretta caretta*, in southeastern U.S. waters

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Somatic growth functions are critical parameters for understanding the life history of a species and for developing management plans for wild populations. Substantial effort has been invested in—and considerable information on growth rates has been gained from—mark-recapture studies of sea turtle populations (Chaloupka and Limpus, 1997; Chaloupka and Musick, 1997; Limpus and Chaloupka, 1997; Bjorndal et al., 2000). Although growth studies based on mark and recapture of individual animals yield direct measures of growth rates, sea turtles have characteristics that make them relatively poor candidates for mark-recapture studies. Sea turtles are relatively slow growing; consequently mark-recapture studies are long-term labor-intensive efforts. The probability of recapturing marked individuals is low in many populations because of the long-range movements and obscure migratory patterns in some lifestages (e.g. posthatchlings in a pelagic habitat), high natural mortality in young lifestages, and high human-induced mortality in juvenile and adult lifestages.

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Length-frequency analysis has been used for many years to estimate growth rates, age structure, and mortality in marine fish and invertebrate populations (Ricker, 1975; Pauly and Morgan, 1987; Hilborn and Walters, 1992). More recently, length-frequency analyses have been used to evaluate somatic growth rates in sea turtles. The accuracy of four length-frequency analysis programs (ELEFAN I, [Holden and Bravington, 1992] Shepherd's length composition analysis [SLCA, Holden and Bravington, 1992], projection matrix method [Holden and Bravington, 1992], and MULTIFAN) for predicting growth rates was tested in a population of green turtles, *Chelonia mydas*, in the southern Bahamas for which growth rates had been measured in a long-term mark and recapture study (Bjorndal and Bolten, 1995; Bjorndal et al., 1995). MULTIFAN successfully estimated growth rates in this population, SLCA was partially successful, and ELEFAN I and the projection matrix method were not successful. In young, pelagic-stage loggerhead sea turtles (*Caretta caretta*), estimates of growth rates generated by MULTIFAN were consistent with results from recaptures of tagged turtles (Bjorndal et al., 2000).

In our study, we generated a growth model for immature loggerhead sea turtles in southeastern U.S. waters between the size at which they begin to recruit in substantial numbers to neritic habitats (46 cm curved carapace length [CCL]) and minimum size at sexual maturity (87 cm CCL). The duration of the growth interval between 46 and 87 cm CCL is critical information for developing management plans and demographic models for this sea turtle, which is listed as a threatened species in the U.S. Endangered Species Act of 1973. This size range includes the large juvenile and subadult lifestages defined in the stage-based population model developed for North Atlantic loggerhead sea turtles (Crouse et al., 1987; Crowder et al., 1994). This stage-based population model has identified survivorship in the large juvenile lifestage as the most critical for population recovery. We based our length-frequency analyses on data collected from hundreds of loggerhead sea turtle carcasses that were measured by the Sea Turtle Stranding and Salvage Network from Florida, Alabama, Mississippi, Louisiana, and Texas between 1988 and 1995.

Methods

Length-frequency data

The Sea Turtle Stranding and Salvage Network (STSSN) is an organized network of individuals who monitor the shoreline and record data on each stranded sea turtle, including date and location of stranding, species, and carapace length (curved or straight carapace length, or both). Carapace length is measured from the anterior point at midline (nuchal scute) to the posterior tip of the supracaudals. The stranding data are compiled and verified by state coordinators and archived at the Southeast Fisheries Science Center (SEFSC) Miami Laboratory (Teas, 1993). We received data on stranded turtles for 1988 through 1995 for Alabama, Mississippi, Louisiana, and Texas from SEFSC and data for 1988 through 1995 for Florida from the Florida Department of Environmental Protection, Florida Marine Research Institute. All turtles known to have been "head-started" (that is, raised in captivity before being released into the wild) were excluded from the analyses because growth rates in captivity, and therefore length-at-age, may be quite different for head-started turtles. We divided the data into two geographic regions: the Atlantic coast of Florida and the U.S. coast of the Gulf of Mexico (Florida, Alabama, Mississippi, Louisiana, and Texas). The Florida coast was divided between Atlantic and Gulf by the STSSN at 80.5°W.

Because most of the data on carapace length were over-the-curve measurements, straight carapace lengths (SCL) were converted to curved carapace lengths (CCL) by using the conversion equation (n=932, r^2=0.97, P<0.001) in Teas (1993)

$$SCL = (0.948 \times CCL) - 1.442.$$

After conversions were completed, all CCL data were rounded to the nearest cm.

We wanted to limit our analyses to the subadult, neritic lifestage that inhabits the coastal waters of the southeastern U.S.; therefore we limited the size range of loggerhead sea turtles from 46 to 87 cm CCL. The lower value was based on length-frequency distributions (Bolten et al., 1993; Bjorndal et al., 2000) that indicated that 46 cm CCL is the size at which these sea turtles begin to recruit to neritic habitats in substantial numbers. The largest subadult size was taken as 87 cm CCL based on Witherington (1986), who reported that 88 cm CCL was the size of the smallest nesting loggerhead sea turtle at Melbourne Beach, Florida. This value is a very conservative division between subadults and adults; many with CCLs greater than 87 cm are still immature. For length-frequency analyses, however, it is better to exclude some subadults than to include many adult animals. Any factor that acts to obscure the modal structure of the sample—such as cessation or near-cessation of growth in older age classes—will decrease the potential for successful length-frequency analysis. If older age classes cannot be distinguished, K (intrinsic growth rate) will be overestimated and the number of age classes underestimated (Terceiro et al., 1992). Because loggerheads essentially stop growing at sexual maturity and because they attain sexual maturity at a range of sizes (Frazer and Ehrhart, 1985), the age classes—or modes—above the minimum size at sexual maturity are obscured and cannot be distinguished in length-frequency analyses.

Kolmogorov-Smirnov analyses were conducted with SPSS software (version 9.0 SPSS, 1996).

Length-frequency analysis

We used MULTIFAN (version 32(f), Otter Research Ltd., 1992) modified to include 30 age classes by Fournier (Otter Research Ltd., 1992). MULTIFAN simultaneously analyzes multiple samples of length-frequency data (Otter Research Ltd., 1992) and uses nonlinear statistical mod-

eling and robust parameter estimation to estimate the parameters of the von Bertalanffy growth function (Fournier et al., 1990, 1991). Log-likelihood objective functions are compared by using maximum likelihood analyses to identify the parameter set for the von Bertalanffy model with the best fit.

The form of the von Bertalanffy equation that was used in the MULTIFAN program is

$$\mu_{j\alpha} = m_1 + (m_N - m_1)\left(\frac{1-\rho^{j-(m(\alpha)-1)/12}}{1-\rho^{N_j}}\right),$$

where $\mu_{j\alpha}$ = the mean length of the age class j turtles in the αth length frequency data vset;

m_1 = the mean length of the first age class;

m_N = the mean length of the last age class;

ρ = the Brody growth coefficient;

$m(\alpha) - 1$ = the number of months after the presumed birth month of the turtle in the αth length-frquency data set; and

N_j = the number of age classes in the data set.

This parameterization of the von Bertalanffy growth equation is derived in Schnute and Fournier (1980).

The MULTIFAN length-frequency program has the following assumptions: 1) growth is described by a von Bertalanffy growth curve; 2) samples represent the structure of the population; 3) recruitment occurs in seasonal pulses, 4) the lengths of animals in each age class are normally distributed; and 5) the standard deviations of the lengths are a simple function of the mean length-at-age.

MULTIFAN requires that initial values for the following parameters be designated as starting points for the iterations: expected number of age classes; expected initial K values; mean length of the mode representing the youngest age class; standard deviation of a distinct mode; and month in which youngest animals recruit to the population. We estimated initial values for expected number of age classes as varying between 2 and 30 years, and for K as 0.01, 0.05, 0.1, and 0.5/yr. The initial estimate for mean length of the youngest age class was 47 cm, and the initial standard deviation of mode width was estimated as 1.5 cm. Because there was a significant trend in standard deviation of length-at-age with increasing length, this parameter was included in the models reported here. April was designated as the month in which youngest turtles recruit into the population because the April samples had the smallest individuals. The CCL data were combined among years by month so that samples were sufficiently large for length-frequency analyses.

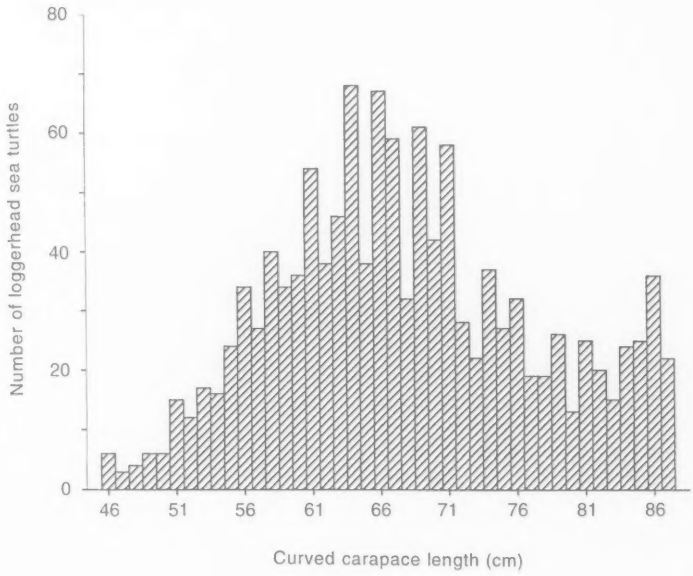

Figure 1

Length-frequency distribution of loggerhead sea turtles stranded along the Atlantic coast of Florida from 1988 through 1995 within the size range of 46 to 87 cm curved carapace length (n=1234).

Results

The length-frequency distributions of loggerhead sea turtles within the size range of 46 to 87 cm CCL that stranded from 1988 through 1995 along the Atlantic coast of Florida (n=1234) and along the U.S. coast of the Gulf of Mexico (Gulf coast of Florida, Alabama, Mississippi, Louisiana, and Texas, n=570) are shown in Figures 1 and 2, respectively. The two distributions are significantly different (Kolmogorov-Smirnov test, Z=3.934, P<0.001), although the relative patterns are similar. We assumed that the length-frequency distributions of stranded sea turtles are representative of the length-frequency distributions of sea turtles in the two regions, although there is potential for sampling bias from incidental capture in commercial fisheries.

For loggerhead sea turtles in both the Florida Atlantic and the Gulf of Mexico, the MULTIFAN analysis estimated that the 46 to 87 cm CCL size range comprises 20 year classes (Table 1, Fig. 3). For both geographic regions, visual inspection revealed that the models fit the length-frequency data well (an example is shown in Fig. 4). We were unable to assess annual variation because we combined data for each month from different years owing to small sample sizes. Also, combining data among years

Table 1

Number of age classes (years) in Atlantic loggerhead sea turtle populations within the size range of 46 to 87 cm curved carapace length. Estimates were calculated from von Bertalanffy growth models presented in the referenced studies. Method is type of data (SC=skeletochronology, MR=mark-recapture, LF=length frequency); n = sample size.

Location	Number of age classes	n	Method	Reference
Chesapeake Bay	13	83	SC	Klinger and Musick, 1995
Cumberland Island, Georgia	11[1]	25[1]	SC	Parham and Zug, 1997
	9[2]	26[2]	SC	Parham and Zug, 1997
Cape Canaveral, Florida	29[3]	51[3]	MR	Schmid, 1995
	26[4]	17[4]	MR	Schmid, 1995
Mosquito Lagoon, Florida	15	28	MR	Frazer and Ehrhart, 1985
Florida, Atlantic Coast	20	1234	LF	This study
Gulf of Mexico	20	570	LF	This study

[1] Based on "1979-new" data set in which correction-factor protocol was used (Parham and Zug, 1997).
[2] Based on "1980" data set in which correction-factor protocol was used (Parham and Zug, 1997).
[3] Based on "all recaptures" data set (Schmid, 1995).
[4] Based on "contract vessel" data set (Schmid, 1995).

could have obscured age-class modes, but because MULTIFAN was able to distinguish modes and the models fitted the data well, this procedure was apparently not a problem.

The von Bertalanffy parameter estimates generated by MULTIFAN for asymptotic length (L_∞) and intrinsic growth rate (K) for the Florida Atlantic were L_∞=118.5 ±0.7 cm and K=0.044 ±0.001/yr and for the Gulf of Mexico were L_∞=113.0 ±0.4 cm and K=0.051 ±0.001/yr. The maximum CCL value recorded for loggerheads nesting in the southeastern United States is 124 cm (Dodd, 1988); therefore the estimates of asymptotic length are reasonable.

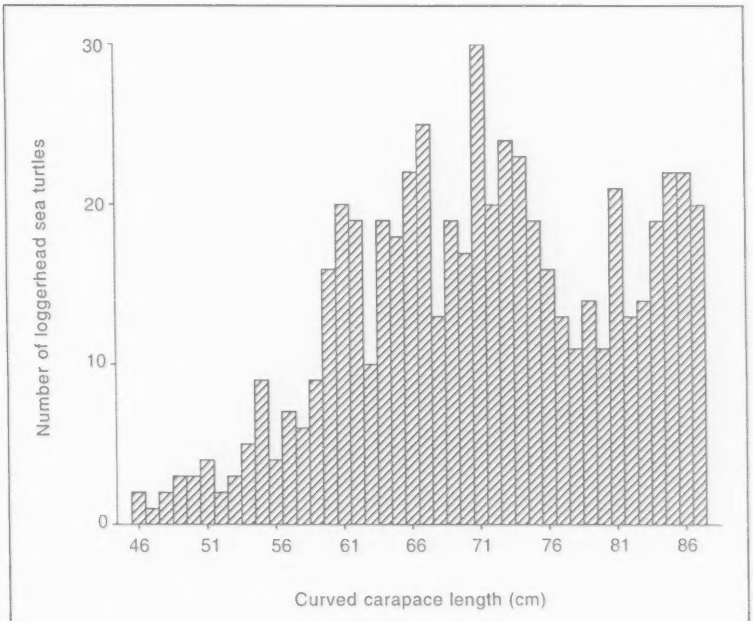

Figure 2

Length-frequency distribution of loggerhead sea turtles stranded along the U.S. coast of the Gulf of Mexico from 1988 through 1995 within the size range of 46 to 87 cm curved carapace length (n=570).

Discussion

Duration of the neritic lifestage

Most loggerhead sea turtles in the North Atlantic recruit to neritic habitats over a size range of 46 to 64 cm CCL (Bjorndal et al., 2000). Size at recruitment will affect duration of the neritic lifestage. From our model, loggerhead sea turtles that recruit at 46 cm CCL will require 20 years to reach 87 cm CCL, whereas those that recruit at 64 cm CCL will require 13 years to grow to 87 cm CCL (Fig. 3). Because loggerhead sea turtles usually remain in neritic habitats after recruiting to these habitats, total duration of the neritic lifestage will include the years subsequent to attaining 87 cm CCL. The demographic ramifications of this variation in size at recruitment should be evaluated.

Other studies have used von Bertalanffy models to evaluate growth in immature loggerhead sea turtles in the Atlantic (Table 1) based on either mark and recapture data (Frazer and Ehrhart, 1985; Schmid, 1995) or skeletochronology data (Klinger and Musick, 1995; Parham and Zug, 1997). Schmid (1995) and Parham and Zug (1997) presented data for a number of data sets and types of calculation. For both studies, the data presented in Table 1 are for the two data sets that Schmid (1995) and Parham and Zug (1997) considered the most representative.

Our estimates of 20 year classes in the size range from 46 to 87 cm CCL fall within the range of values of 9 to 29 years that we calculated from the von Bertalanffy growth equations presented in other studies (Table 1). There is no geographic trend in these estimates.

Von Bertalanffy growth model

MULTIFAN uses a von Bertalanffy growth model as derived by Schnute and Fournier (1980). Concerns about the application of the von Bertalanffy model to sea turtle populations have been discussed elsewhere (Bjorndal and Bolten, 1988; Chaloupka and Musick, 1997). A major concern is the use of the von Bertalanffy model to extrapolate outside the size range of a study (Day and Taylor, 1997), which has been a common practice in estimating age at sexual maturity in sea turtle populations (reviewed in Chaloupka and Musick, 1997). However, within a growth phase that exhibits monotonic decline—that is, for a given size range of a population with similar habitats and diet and that has declining growth rates with increasing body size—the von Bertalanffy model may provide reasonable estimates of growth rates and number of age classes. Green turtles in the southern Bahamas have a monotonic nonlinear declining function for SCL-specific growth rates in a size range of 30 to 70 cm SCL as determined from nonlinear regression of mark-recapture data (Bjorndal et al., 2000). Length-frequency analyses with MULTIFAN yielded the same estimates as the nonlinear regression analysis for growth rates and number of age classes between 30 and 70 cm SCL for that population (Bjorndal et al., 2000). Similar trends of decreasing growth rates with increasing size have been reported from mark-recapture studies in Atlantic loggerhead sea turtles (summarized in Parham and Zug, 1997). In addition, use of the von Bertalanffy model within the studied size range is supported by the similarity between growth rates generated from MULTIFAN and those calculated from recaptures of tagged pelagic-stage loggerhead sea turtles (Bjorndal et al., 2000). As growth data accumulate for sea turtle populations, appropriate growth functions—which may well be polyphasic (Chaloupka and Zug, 1997; Chaloupka, 1998) as a result of habitat shifts—can be incorporated into the length-frequency software.

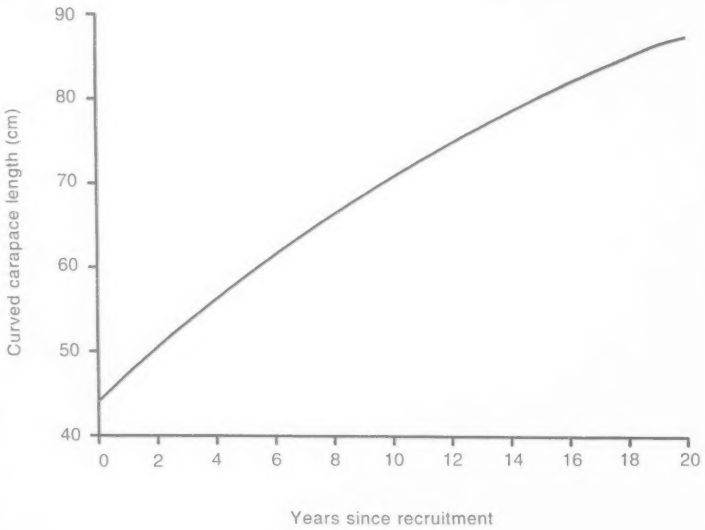

Figure 3

Age-specific von Bertalanffy growth model generated by MULTIFAN for loggerhead sea turtles stranded along the Atlantic coast of Florida from 1988 through 1995 within the size range of 46 to 87-cm curved carapace length. The growth curve for loggerhead sea turtles stranded in the Gulf of Mexico is not plotted because it is indistinguishable from the line plotted for the Atlantic coast of Florida. Age is defined as years since recruitment to neritic habitats at a size of 46 cm curved carapace length.

Age at sexual maturity

An estimate of the number of years to grow to 87 cm CCL may be generated by combining our results (20 year classes between 46 and 87 cm CCL) with those from a growth study in pelagic-stage loggerhead sea turtles in the North Atlantic (Bjorndal et al., 2000). In that study, based on length-frequency analyses and mark-recapture data, the age of loggerheads with a CCL of 46 cm was estimated to be 6.5 years. Therefore, an 87-cm loggerhead sea turtle would be approximately 26.5 years old.

This estimate of 26.5 years at 87 cm CCL should not be used as an estimate of age at sexual maturity. Although we used 87 cm CCL to represent the largest subadult in our study, as explained above, we used a conservative estimate to exclude almost all adults from the sample to avoid obscured modes in the length-frequency distributions. Many loggerhead sea turtles will reach sexual maturity at lengths much greater than 87 cm CCL, and because growth rates are slow in these large subadults, the average age at sexual maturity would be substantially greater than the average age at 87 cm CCL.

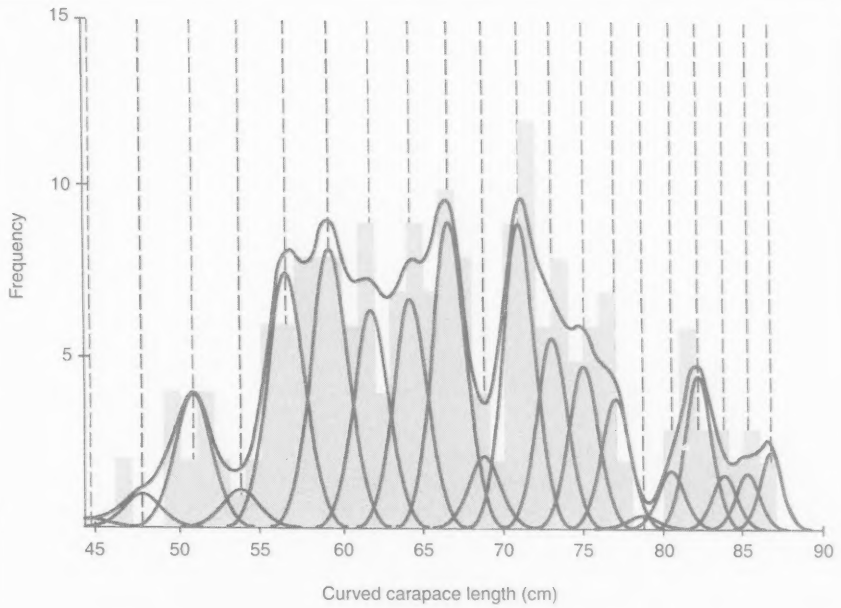

Figure 4

Fit of model to length-frequency data for loggerhead sea turtles stranded along the Atlantic coast of Florida in May (n=203). The dashed vertical lines represent estimated mean lengths-at-age. Both the estimated aggregate (upper line) and the estimated length distribution for each age class are shown. Histogram represents length-frequency data.

Conclusion

With length-frequency analyses, we estimated that growth from 46 to 87 cm CCL in Atlantic loggerhead sea turtles requires 20 years. This estimate falls within the range of estimates of 9 to 29 years that we calculated from other studies based on mark-recapture and skeletochronology. Because survivorship in this size class has been identified as a critical parameter for population recovery (Crouse et al., 1987; Crowder et al., 1994), accurate estimates for the duration of the stage are essential for developing successful management plans. Research must be continued to refine this estimate.

Conservation of loggerhead sea turtles that spend an extended period of time in nearshore habitats prior to reaching sexual maturity is compromised. Numerous and significant threats—including incidental capture in commercial fishing operations, collisions with motorized vessels, dredging operations, exposure to pollutants and biotoxins, and habitat degradation—are present in nearshore developmental habitats. There is a high probability that these turtles will encounter one or more of these threats during their maturation period (National Research Council, 1990; Eckert, 1995; Lutcavage et al., 1997). To be successful, recovery activities must be sustained for long periods of time, and long-term monitoring programs to assess the status of populations of juvenile loggerhead sea turtles in U.S. waters must be established. Because current loggerhead population assessments depend upon the numbers of nesting females or nests, two or more decades must pass before results of recovery activities aimed at the earliest age classes in nearshore waters can be evaluated.

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A study of catches in a fleet of "ghost-fishing" pots

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Abstract—Pots are a form of trap used to capture fishes, crustaceans, or gastropod mollusks. Occasionally, these traps are lost at sea, where they have the potential to fish for many years because they are constructed of robust manmade materials. The present study quantified the mortality and number of animals caught by a fleet of crustacean pots (12 pots) that were set on the seabed and left to fish continually in a manner designed to simulate ghost-fishing off the coast of Wales, UK. The bait originally placed in the pots was consumed within 28 days of the beginning of the experiment. Spider crabs and brown crabs dominated the catches within the pots throughout the experiment. The CPUE of spider and brown crabs declined as an inverse function of time and reached a minimum between 125 to 270 days after initial deployment in August 1995. After this period, CPUE increased again, although it did not attain the rates associated with the beginning of the experiment. The fleet of twelve pots caught a minimum of 7.08 spider and 6.06 brown crabs per pot per year and killed a minimum of 6.06 brown crabs and 0.44 lobsters per pot per year. Other species caught in the traps included velvet swimming crab, lobster, ballan wrasse, dogfish, and triggerfish. The pots continued to catch animals into the second year of the experiment. These results suggest that pots have the potential to fish for extended periods. The wider use of biodegradable escape panels is recommended because currently there is no national legislation in the UK to enforce such escape measures.

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Static fishing gear, such as gill and trammel nets and pots or traps, are considered to be highly selective for target species. In addition, these gears might be considered to be environmentally friendly because they cause relatively little disturbance of seabed communities when compared with towed bottom-fishing gears (Jennings and Kaiser, 1998). However, set nets or pots can be lost as a result of bad weather, ice chafing and cutting mooring ropes, pots being snagged on seabed obstructions, or pots being inadvertently towed away by mobile fishing gears. The lost gear may then continue to fish indiscriminately, which is a phenomenon known as "ghost-fishing." In contrast with the numerous records of bird, reptile, and cetacean entanglement in set gears (see Dayton et al., 1995 and references therein), little is known about the frequency of static gear loss or for how long such gears continue to fish. The paucity of information relating to this phenomenon results from the reluctance of fishermen to report such incidents and the difficulty in undertaking long-term studies in a realistic manner.

Estimates of the proportion of nets lost from commercial fleets appear to be substantial. Approximately 7000 km of drift nets (20–30% of the total nets set each day) were lost per year in a North Pacific fishery (Eisenbud, 1985). Considerable numbers of pots are also lost each year from some fisheries, although estimates vary greatly between different studies. For example, Kruse and Kimker[1] estimated that that in 1990 and 1991, 31,600 pots per year were lost in the North American Bristol Bay king crab (*Paralithodes camtschaticus*) fishery, whereas Paul et al. (1994) and Stevens (1996) estimated that losses from the same fishery were respectively 20,000 and 7000 pots per year. Breen (1987) estimated that 11% of the traps used in the Dungeness crab *Cancer magister* fishery of British Columbia are lost each year. Modern com-

[1] Kruse, G. H., and A. Kimker. 1993. Degradable escape machanisms for pot gear: a summary report to the Alaska Board of Fisheries. Regional Information Report 5J93-01, 23 p. Alaska Department of Fish and Game (ADFG), 211 Mission Rd. Kodiak, AK 99615, Alaska.

mercial set nets and pots are made of nonbiodegradable man-made materials. As a result, lost nets and pots have the potential to persist and continue to fish in the marine environment for several years depending upon the prevailing environmental conditions (Breen, 1987; Carr et al., 1990; Kaiser et al., 1996). Set nets that are lost in areas exposed to large swell and storm activity (e.g. off the North west coast of Spain) are rapidly destroyed (Puente[2]). Nets lost in shallow, clear water are rapidly overgrown with encrusting biota that makes them more visible and reduces their fishing capabilities (Erzini et al., 1997). However, when static gear becomes snagged on rocks that hold it in place, or is lost in deep water in a relatively stable environment, it may continue to fish for more than a year (Carr et al., 1990; Kaiser et al., 1996).

Lost pots are likely to continue fishing for longer than static nets because they are constructed either entirely of metal or of thick netting attached to a rigid frame. Exactly how long lost pots are likely to continue fishing remains unquantified.

The present study was undertaken in grounds where pot gear is typically used—at a site within the Skomer Marine Nature Reserve (MNR), Wales, UK. MNR staff have recorded the occurrence of lost pots over a number of years within the waters of the reserve. Most observations were of single pots in locations sheltered from strong water movement. Such pots were usually heavily overgrown with sessile biota, indicating that they had been submerged for at least 6 months. Lost pots within the MNR have been reported by recreational divers who have described occasional large resident catches of crustacea and fish, such as ballan wrasse (*Labrus bergylta*) and conger eels (*Conger conger*). The objectives of our study were 1) to quantify the number of organisms removed by a fleet of lost pots; 2) to describe changes in catch rate over time; and 3) to record any deterioration in the integrity of the fishing gear.

Methods

Site selection

The study site was located in the Skomer MNR off the coast of Pembrokeshire, Wales (Fig. 1). This site was representative of those fished by locally based inshore pot fishermen. Maximum tidal streams ranged from 2 to 3 knots on spring tides. The site was sheltered from heavy wave action and the seabed comprised mainly boulders to a depth of 15 m below the lowest recorded astronomical tidal height. Below this depth, the substratum was composed of mixed coarse sediments, cobbles and boulders, and occasional bedrock outcrops.

Gear and deployment

The gear comprised 12 parlor pots of approximate dimensions 750 mm × 500 mm × 500 mm with a top-mounted cylindrical entrance ring made of plastic (Fig. 1). Two sizes of entrance ring were used, either 200 mm (n=7) or 240 mm (n=5) diameter. In our analysis we made no attempt to differentiate catches based on entrance ring size because size of trap entrance was not a major consideration in our experiment. The pots were attached to a mainline by using 3.5-m lengths of polypropylene rope at intervals of 18 m. This configuration of the gear is the normal fishing practice used in the UK (Fig. 1). The fleet of pots was anchored at each end with a 75-kg weight and marked with surface marker buoys (Fig. 1). Each pot was baited with the corpse of a thornback ray (*Raja clavata*) (its wings having been removed) and attached to the entrance ring with a rubber band. On each sampling occasion the position of the fleet of pots was determined by a differential global positioning system. The pots were deployed on 4 August 1995. During deployment, the mainline was checked to see that it was tight between each of the pots when shot from the boat. Gear deployment was undertaken in consultation with a local professional pot fisherman. Divers surveyed the fleet of pots immediately after it had been shot away to confirm that the gear was deployed on the seabed correctly and to record the depth at which each pot had settled. It was thought important to record pot depth during the study because pots lost in shallow water might be more prone to destruction by wave action, whereas progressive movement of the pots into deeper water might prolong their fishing capabilities. Although it would have been preferable to have deployed replicate fleets of pots in different habitats, the logistics of diver-based observations and the need to minimize the adverse effects of the experiment on local populations of animals meant that this was neither possible nor considered ethically acceptable. Indeed, the ethical considerations of undertaking such an experiment in an MNR meant that 3 pots were removed from the experiment after 88 days and a further 3 pots removed after 270 days of fishing to minimize animal deaths associated with the study.

Data recording

Observations on each of the pots were recorded by divers 1, 4, 12, 27, 40, 69, 88, 101, 125, 270, 333, 369, and 398 days after initial deployment. Divers undertook the following tasks:

1 recorded the depth (adjusted for tidal height) of pots throughout the experiment.
2 recorded the identity of the catch in each pot.
3 tagged newly captured crustaceans (brown crab [*Cancer pagurus*] spider crab [*Maja squinado*] and the lobster *Homarus gammarus*) on each sampling occasion with coded and colored cable ties on their appendages so that they could be distinguished from newly captured animals (without tags) on subsequent occasions.

The identification of previously caught individual lobsters, brown crabs, and spider crabs caught in the pots was checked by inspection of the species-specific colored and coded tags placed on different body parts of each animal during a previous sampling routine. It was not possible to tag smaller crustaceans such as the velvet swim-

[2] Puente, E. 1997. Personal commun. Isla de Txatxarramendi, s/n 48395 Sukarrieta (Bizkaia), Spain.

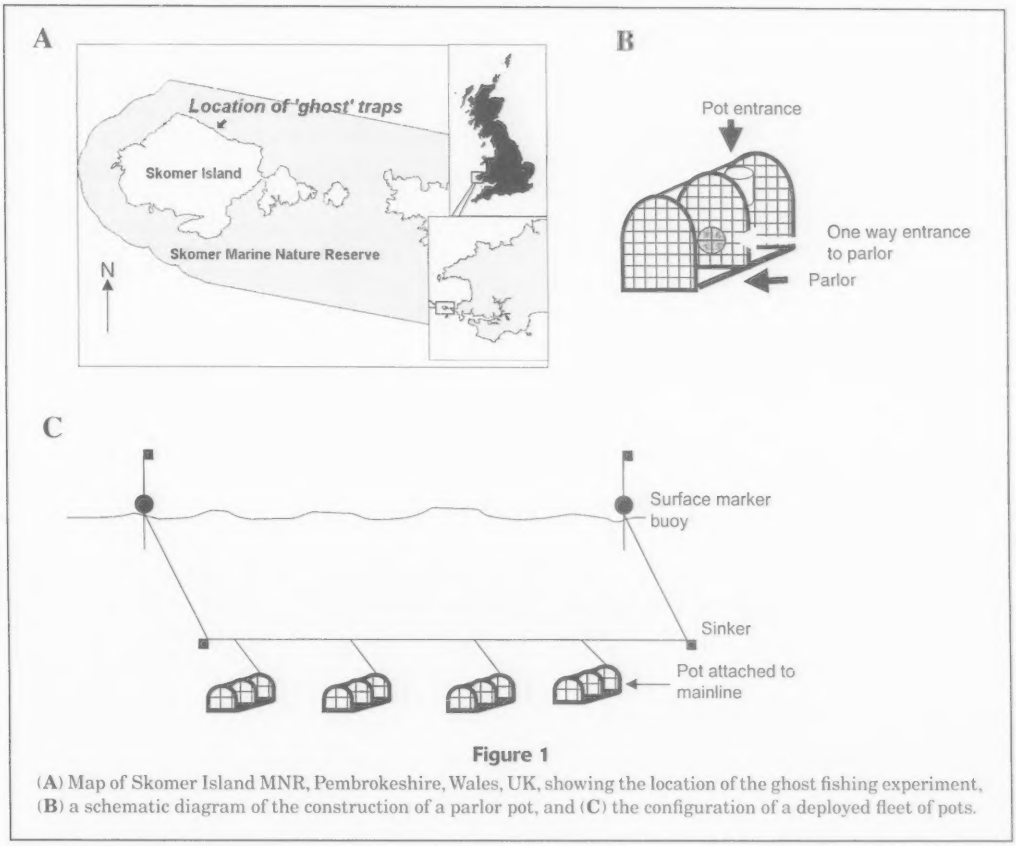

Figure 1

(**A**) Map of Skomer Island MNR, Pembrokeshire, Wales, UK, showing the location of the ghost fishing experiment, (**B**) a schematic diagram of the construction of a parlor pot, and (**C**) the configuration of a deployed fleet of pots.

ming crab (*Liocarcinus puber*) and fish were never tagged. However, fish were readily identifiable on consecutive occasions from the injuries sustained while resident in the pots. These injuries most frequently occurred as wounds on the head region that were sustained as the fish tried to escape through the pot meshes. Records were made of the presence and condition of bait on each occasion. Pot depth was estimated from divers' depth gauges and corrected for the state of tide from appropriate tide-tables.

Statistical analyses

Variation in the total resident catch (all species) within the pots at each time interval was analyzed by using a GLM (general linear modeling) ANOVA with time as the independent variable. Catch rates were calculated as the number of newly captured animals caught per pot and recorded by divers on each consecutive sampling occasion. It was not possible to standardize the sampling time interval because weather conditions and water visibility during the winter period were not conducive to regular sampling. Because the intersample period and number of pots varied throughout the experiment, the catch data were expressed as catch-per-unit-of-effort (CPUE) data with the following formula:

$$CPUE = N_j / \left(E_p (t_j - t_i)\right),$$

where N_j = the number of newly caught animals;
E_p = number of pots fishing; and
$t_j - t_i$ = the time interval since the previous observation (t_i).

The existence of a relationship between the decline in catch rate with time was determined by using nonlinear regression analysis in the SPSS statistical software package (SPSS, 1998). These analyses were performed only for brown and spider crabs because other animals were caught in insufficient numbers for meaningful analyses. Preliminary examination of the data suggested that the capture rate for the crab species differed with season; hence the regression analyses were undertaken by using only the data for the first 125 days of the experiment. Furthermore, there was a long period without direct observations from 125 to 270 days after initial deployment of the gear. Catch rate does not provide an indication of the total actual mortality of individuals associated with the ghost-fishing pots. Mortality was confirmed when divers observed the remains of individuals and their tags either at the bottom of the pot, or on the seabed nearby, because both the tags and dead animal fragments were small

Table 1

Resident catches (all species) in each of the twelve pots in the experimental fleet observed after initial deployment of gear at time intervals from August 1995 to September 1996. Mean resident catch per pot is also shown. "R" indicates those pots that were removed at each time interval

		Pot number												
Month	Day	1	2	3	4	5	6	7	8	9	10	11	12	Mean ± 95% CI
Aug	1	1	2	0	0	1	4	4	1	4	2	2	0	1.75 ±0.87
Aug	4	2	2	1	0	2	4	4	1	4	3	4	1	2.33 ±0.81
Aug	13	3	2	2	2	3	4	4	4	6	0	4	0	2.83 ±0.99
Aug	27	2	2	3	3	4	7	4	6	5	1	3	2	3.50 ±1.01
Sep	40	0	2	3	3	4	5	4	6	5	1	3	1	3.08 ±1.04
Oct	69	0	2	6	3	5	7	5	6	7	1	1	3	3.83 ±1.40
Nov	88	0	2	9	4	5	7	3	5	7	1	1	2	3.83 ±1.60
Nov	101	R	3	8	R	6	6	3	R	7	1	1	2	4.11 ±1.74
Dec	125	R	3	5	R	6	2	5	R	7	2	2	1	3.67 ±1.39
May	270	R	1	0	R	5	2	5	R	2	0	0	0	1.67 ±1.65
Jul	333	R	5	2	R	3	R	4	R	4	0	R	R	3.00 ±1.17
Aug	369	R	7	0	R	2	R	5	R	3	2	R	R	3.17 ±1.62
Sep	398	R	7	0	R	2	R	5	R	3	2	R	R	3.17 ±1.62

enough to pass through the meshes of the pots. Thus we were able to quantify the minimum mortality of animals captured per pot per year for the data up to the first 369 days (approximately 12 months) after initial deployment.

The effect of substratum type on the movement of pots on the seabed was analyzed for the first 7 observation periods by using one-way ANOVA. Data from the remaining observation periods were not used because some of the pots were removed after the seventh sampling date. Three different substratum categories were used: rock and large boulders; medium boulders and cobbles; and mixed sediments.

Results

The bait within the pots remained secure during their deployment. The bait was consumed rapidly, and by day 13 only remnants of the bait were observed in 9 of the pots, and by day 27 only 1 pot had any remnants of bait. Throughout the experiment, none of the pots became detached from the mainline between the sinkers. Pot movement was greatest in the first few weeks after deployment and was related to seabed topography. The entire fleet of pots tended to move in a north-westerly direction in line with the prevailing tidal currents as determined from the position of the surface marker buoys. Substratum type did not affect the extent to which the individual pots moved on average during the first 88 days of the experiment (ANOVA, $F_{2,59}=0.62$, $P=0.56$).

Throughout the experiment seven different species were captured in the pots. Divers observed that some animals were always resident in the pots because previously observed animals were frequently observed on subsequent sampling dates. The number of animals resident in the pots did not differ significantly between different observation periods (Table 1, GLM $F_{12,112}=1.07$, $P=0.39$). This finding suggests that as animals died or escaped, they were replaced by new catches. Only spider and brown crabs were captured in sufficient numbers for more detailed analyses. Analyses of the CPUE up to 125 days after initial deployment of the pots revealed that the CPUE decreased significantly for spider crab and brown crab (Fig. 2). The best relationship between the decline in CPUE with time was given by the following relationships:

$$\textit{CPUE spider crab} = 0.0216 + (0.377/\text{day}) \quad [r=0.97, F_{1,7}=236.7, P<0.0001],$$

$$\textit{CPUE brown crab} = 0.0205 + (0.244/\text{day}) \quad [r=0.92, F_{1,7}=77.5, P<0.0001].$$

It is clear from Figure 2 that the CPUE for spider crab and brown crab declined to a minimum rate between 125 and 270 days after initial deployment and then increased rapidly before decreasing again. The regression equation used to calculate the total predicted catch for the first 125 days of the experiment gives a catch of 4.74 spider crabs and 3.88 brown crabs per pot.

Catch rate, however, does not provide an indication of the total mortality of animals associated with the ghost-fishing pots. We were able to confirm annual mortality only per pot for lobster and brown crabs, of which 100% died because divers retrieved all the tags deployed on individual lobsters and brown crabs in the pots (Table 1). A conservative estimate of total mortality indicates that each pot killed on average 6.06 brown crabs and 0.44 lobsters per year (Table 2). This finding takes no account of animals

Table 2

Newly captured animals for the entire fleet of pots at various time intervals after first deployment of gear. For ethical reasons, after day 88, the number of pots was reduced to 9 and after day 270 the number of pots was further reduced to 6. Mean catch per pot per year was calculated from the sum of the total new catch divided by the number of pots fishing at each time interval.

		Days from original deployment												
		1	4	12	27	40	69	88	101	125	270	333	369	
		Number of pots fishing												
Species	Common name	12	12	12	12	12	12	12	9	9	9	6	6	Mean catch per pot per year
Maja squinado	spider crab	15	3	9	10	6	7	3	2	0	1	8	6	7.08
Cancer pagurus	brown crab	3	5	5	3	3	9	4	0	3	8	7	6	6.06[1]
Necora puber	velvet swimming crab	1	0	1	0	0	0	0	2	2	0	0	0	0.61
Homarus gammarus	lobster	2	1	1	0	0	0	0	0	1	0	0	0	0.44[1]
Labrus bergylta	ballan wrasse	0	0	0	1	0	0	2	0	1	1	4	5	1.97
Ballistes carolinensis	triggerfish	0	0	0	0	0	0	1	0	0	0	0	0	0.08
Scyliorhinus canicula	lesser-spotted dogfish	0	0	0	0	0	0	1	0	0	0	0	0	0.08

[1] indicates those animals for which all observed catches died.

that may have entered the pots and died without being observed by the divers.

Discusssion

The results of this experiment demonstrate that lost pots can continue to fish for many months after the bait within them has been consumed. There was no sign of deterioration in the integrity of the pots throughout the study. Several "ghost-fishing" pots were found in close proximity to the experimental fleet. This discovery emphasized the practicality of our study and confirmed that location of our experiment was representative of sites used by pot fishermen and that pot losses do occur in this area.

Spider and brown crabs dominated the catches, whereas lobster, velvet swimming crab, and fishes were caught less frequently. The rate of decline of the CPUEs for spider and brown crabs both followed similar patterns. We extrapolated the CPUE for only the first 125 days of the experiment because our own observations indicated that spider crabs migrate into shallower waters around Skomer to breed in the late spring and early summer. Consequently, catches of spider crab were high in August and tailed off as the experiment extended into autumn and winter and the spider crabs migrated farther offshore. In contrast, brown crabs are resident throughout the year in the Skomer MNR and although the CPUE was low during the winter period, it is possible that they continued to be caught sporadically between days 125 and 270. A second pulse of spider crab and brown crab catches occurred 333 days after initial deployment of the pots, which may be linked to rising water temperatures that occur in late spring and early summer (Fig. 2).

We were able to confirm mortality only for lobster and brown crabs (0.44 lobster and 6.06 brown crab per pot per

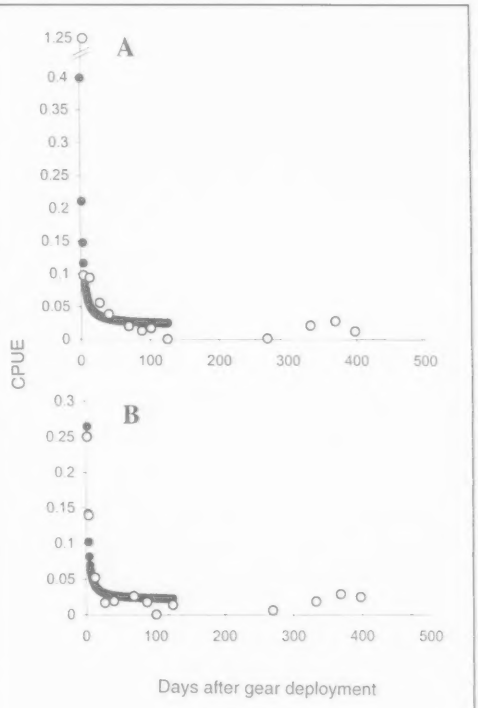

Figure 2

The catch per unit of effort (CPUE) for (**A**) spider crabs and (**B**) brown crabs on each of the sampling dates (open circles). The closed circles represent the predicted values for CPUE as determined from the regression relationships (see text).

Table 3

Bylaws currently in operation in UK waters pertaining to the use of escape gaps and pot design.

Cumbria Sea Fisheries Committee Bylaw No. 25: No person shall use or cause to be used for the purpose of fishing for seafish or crustacea any pot, creel or trap constructed of whatever material unless:

- it has at least one unobstructed escape gap located in the lowest part of the pot, creel or trap or in the case of a parlour pot the parlour area; and
- is so designed and constructed that each escape gap is of sufficient size that there may be easily passed through the escape gap and completely passed in to the pot, creel or trap a rigid boxed shaped gauge which shall be a gauge 74 mm wide, 44 mm high and 100 mm long.

States of Jersey Requirements of escape gaps in parlour pots: No person shall use or cause to be used for the purpose of fishing for seafish any parlour pot, of whatever material constructed, unless:

- it has a least one unobstructed escape gap which shall be located in the lowest part of the parlour areas on a side or sides of the parlour or the bottom of the parlour pot; and
- is so designed and constructed that each escape gap is of sufficient size that there may be easily passed through the escape gap and completely inserted into the parlour pot, whether the parlour pot is wet or dry, a rigid boxed shaped gauge which –
  - in the case of an escape gap located on a side of the parlour pot, shall be a gauge 79 mm wide, 44 mm high and 100 mm long; and
  - in the case of an escape gap located on the bottom of the parlour pot, shall be a gauge 199 mm wide, 44 mm high and 100 mm long.

year). Currently, there is no information on the frequency of pot loss in the UK; hence it is presently not possible to speculate about the annual death rate of crabs and lobsters from ghost-fishing in the UK. Financial losses to the industry are potentially high because lobsters command high prices (up to U.S. $12 per kg) whereas brown crab market prices have fluctuated between $0.60 and $1.60 per kg in recent years. However, there is no market for spider crab in the UK and only a sporadic overseas market for this species in countries such as Portugal and Spain.

All of the initial bait was exhausted after day 27. Presumably, as pot residents die, they act as bait luring more animals into the traps. We suspect that the fish that died would provide a ready source of food for trapped Crustacea, an observation that concurs with those in related studies (Kaiser et al., 1996). Recent studies have shown that a similar pattern of capture is observed in lost set nets. Over the first few days, catches decline almost exponentially. Then, for the next few weeks, the decaying bodies of fishes and Crustacea attract large number of scavenging crustaceans that also become trapped in the gear. Thereafter, there appears to be a continuous cycle of capture, decay, and attraction for as long as the gear remains intact (Carr et al., 1990; Kaiser et al., 1996).

It is interesting to note that ballan wrasse were caught in greater numbers in the traps during the last 65 days of the experiment, perhaps when there were fewer Crustacea in the pots compared with the beginning of the experiment. Wrasse seemed to develop wounds on their heads that resulted from their attempts to push through the mesh of the pot. These became severely infected and we believe contributed to their eventual death. Wrasse may become trapped within pots when they seek shelter.

Our estimates of capture rate are probably conservative because some animals may escape the traps. Divers found several spider crabs that had been tagged in one pot, but on the subsequent sampling occasion, they were recorded in a different pot. These animals had escaped one trap only to be captured in another. Similarly, Guillory (1993) found that up to 42% of blue crabs (*Callinectes sapidus*) escaped traps. The "ghost-fishing" potential of pots also varies for different fisheries and pot designs. For example, Parrish and Kazama (1992) found that the majority of Hawaiian spiny lobster (*Palinurus marginatus*) and slipper lobster (*Scyllarides squammosus*) were able to escape traps, whereas parlor-type traps lead to mortalities of 12–25% for American lobster (*Homarus americanus*) (Smolowitz, 1978). Catches in pots are also affected by the identity of the initial occupants. For example, Miller and Addison (1995) found that the presence of American lobsters within a pot deters entry of smaller crab species. Similarly, the presence of recently molted brown crabs within pots deterred entry of conspecifics (Addison, 1995).

Potential losses from the brown crab fishery due to ghost-fishing gear could be large. These losses are undesirable both from a conservation and economic point of view. Pot fisheries target species with high individual value, hence each loss is expensive. Fishermen in set-net fisheries have taken their own steps to reduce this phenomenon leading to a grapnel survey of the seabed on Georges Bank and retrieval of 341 actively fishing ghost nets from 286 tows (Brothers[3]). In some fisheries in North America, fishermen must fit their pots with escape gaps or escape panels that either biodegrade and fall out of the pot after a certain length of time, or that have degradable escape panel clips. In contrast, there is no UK legislation to force

[3] Brothers, G. 1992. Lost or abandoned fishing gear in the Newfoundland aquatic environment. Report of the Symposium on Marine Stewardship in the Northwest Atlantic, Department of Fisheries and Oceans, St. Johns, Newfoundland, Canada.

fishermen to use these conservation measures in conjunction with the traps, with the exception of bylaws in two areas (Table 3). Conservation measures such as these are relatively inexpensive to introduce and would greatly reduce losses from the fishery of commercially important species, such as lobster and brown crab, as well as species of conservation interest such as ballan wrasse.

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Age, growth, and mortality of gray snapper, *Lutjanus griseus*, from the east coast of Florida

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Abstract–Gray snapper, *Lutjanus griseus*, were sampled from recreational headboat and commercial landings along the east coast of Florida, 1994–97. Fish were weighed (g) and measured (total length, TL, in mm), and sagittal otoliths were removed for aging. Marginal increment analysis on sectioned otoliths (n=1243) confirmed annulus formation in June and July. The oldest fish examined was 24 years old and measured 760 mm TL. Weight-length relations were not significantly different by sex. Weight-length relations were significantly different (F=39.198, P<0.001, df=10,705) for fish measured from the headboat survey from 1982–97 between north Florida ($W=8.4 \times 10^{-9} \times TL^{3.08}$, n=4034) and south Florida ($W=5.45 \times 10^{-9} \times TL^{3.15}$, n=6670), where W = total weight (kg). The TL-otolith radius (OR) relationships were described by the following equations: $TL = (10.02 \times OR) - 52.98$ (r^2=0.90, n=519, north Florida), and $TL = (9.90 \times OR) - 91.68$ (r^2=0.78, n=724, south Florida). Mean lengths at age from back-calculations to the last annulus ranged from 121 mm at the end of age 1 to 740 mm at age 24 for north Florida, and 227 mm at age 2 to 495 mm at age 15 for south Florida. The von Bertalanffy growth equations were $L_t = 717 \times (1-e^{(-0.17\,(t\,+\,0.025))})$ for north Florida and $L_t=625 \times (1 - e^{(-0.13\,(t\,+\,1.330))})$ for south Florida. Estimates of M ranged from 0.14 to 0.43 for north Florida and from 0.29 to 0.38 for south Florida. Estimates of Z averaged 0.34 for north Florida and 0.95 for south Florida. Recruitment to the fisheries occurred between ages 5 and 8 for north Florida and ages 4 and 5 for south Florida. Estimates of F for gray snapper by area were 0.16 for north Florida and 0.66 for south Florida.

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The gray snapper, *Lutjanus griseus*, is a moderate-size (to 8 kg) snapper (Lutjanidae) widely distributed in the western Atlantic from Florida through Brazil, including Bermuda, the Caribbean and the northern Gulf of Mexico (Robins et al., 1986). Juveniles have been reported from as far north as Massachusetts (Sumner et al., 1911), and transforming gray snapper larvae have been caught in ichthyoplankton samples collected at Ocracoke and Oregon Inlets, North Carolina (Hettler and Barker, 1993). Adults are rarely caught in the fisheries of North Carolina; the larvae appear to be Gulf Stream exports and do not survive winter temperatures. Gray snapper occupy a variety of habitats during their life cycle. Adults are found near irregular, complex habitats, such as coral reefs, shipwrecks, rocky outcroppings and ledges, and other natural livebottom areas (Miller and Richards, 1980). Spawning occurs offshore, and eggs and larvae are transported into estuarine, shallow seagrass, and mangrove nursery areas by favorable currents. Larvae, juveniles, and smaller adults are found inshore in seagrass beds and around mangrove thickets, pilings, seawalls, and jetties. While they inhabit inshore areas, these younger fish are subject to fishing pressure from recreational fishermen. After moving offshore between the ages of 3 and 4 (Rutherford et al., 1983), gray snapper are caught by headboat[1] and commercial fisheries. The primary gear used in all fisheries for gray snapper is vertical hook-and-line gear.

Several investigators have conducted age-growth studies of gray snapper, but most have been restricted by limited geographic samples or gear types. Croker (1962), Starck and Schroeder (1970), and Rutherford et al. (1983) conducted age-growth studies on gray snapper using scales from limited areas in the Florida Keys and Florida Bay; all validated their aging techniques with marginal increment analysis. Manooch and Matheson (1981) aged otolith sections of gray snapper from headboat landings along the entire east coast of Florida but did not validate their aging method. Johnson et al. (1994) described age and growth with fish collected from recreational and commercial landings from Ft. Pierce, Florida, through Louisiana but failed to validate their aging method.

The bulk of gray snapper landings in the U. S. South Atlantic (North Carolina–Florida Keys) occurs in Florida. Combined landings of gray snapper from headboat,[2] private recreational and charterboat[3] and commercial[4] fisheries of Florida's east coast averaged 493,895 kg annually between 1986 and 1997. Average annual landings from the south Florida area (Ft. Pierce through the Dry Tortugas; 412,279 kg) were five times greater than those from north Florida (Fernandina Beach through Sebastian; 81,616 kg). The species is highly

[1] A vessel for hire which charges each angler on a per-person, or "per-head" basis.
[2] South Atlantic Headboat Survey. 1998. Unpubl. data. Administered by National Marine Fisheries Service (NMFS), 101 Pivers Island Rd., Beaufort NC 28516-9722.
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[4] General Canvass Landings Survey. 1998. Unpubl. data. Administered by NMFS, Southeast Fisheries Science Center (SEFSC), 75 Virginia Beach Dr., Miami, FL 33149.

valued by anglers for its fighting ability at all sizes (Manooch, 1984). Recreational landings averaged 60,685 kg for north Florida compared with 290,266 kg for south Florida annually between 1986 and 1997. Commercial landings averaged 20,931 kg for north Florida and 122,013 kg for south Florida for the years 1986–97.

In this study I describe the growth of gray snapper landed from the headboat and commercial fisheries of the east coast of Florida, including the Atlantic waters of Monroe County, FL. I attempt 1) to describe the age and growth of gray snapper from the east coast of Florida, 2) to validate growth increments on otoliths as annuli, 3) to estimate natural mortality (M), and 4) to estimate total mortality (Z) from catch curve analysis. I also compare size at age, growth rates, and mortality rates between the fish in the northern (Indian River County northward) and southern portions of Florida. I undertook this study to provide fishery managers with a current, validated age-growth study, not restricted in either fishery or geographic scope, to use in current stock assessments.

Materials and methods

Gray snapper were sampled from the landings of headboats and commercial fishing vessels from St. Augustine, Florida, through the Florida Keys by National Marine Fisheries Service (NMFS) port samplers from 1994 to 1997. Samples were not available from the Marine Recreational Fisheries Statistics Survey (MRFSS) owing to logistical and contractual problems. Fish samples were taken as available, independent of size, sex, or season. The left sagittal otolith was removed from each fish, rinsed with water, and stored dry. Otoliths were sectioned according to the methods of Potts and Manooch (1995).

I sorted the sectioned otoliths by 50-mm-TL intervals and read them in ascending order, as an aid in determining size at first annulus formation. Reflected light revealed alternating opaque and translucent rings. Opaque rings were presumed to be annuli and ages (in years) were assigned to specimens equal to the number of opaque rings. I measured the distance from the focus to the edge (otolith radius), the focus to successive opaque rings (annular measurements), and the distance between the distal edge of the last opaque zone and the otolith edge (marginal increment).

I analyzed marginal increments to validate the annual periodicity of ring deposition. Monthly mean marginal increments were calculated by age and for all ages combined. Means were plotted against month of capture, the minima indicating the month of annulus formation.

I regressed fish total weight (W) on fish total length (TL), by area, using all gray snapper sampled by the headboat survey from 1982 to 1997 (n=10,705). I examined both a direct nonlinear fit by using nonlinear least squares estimation (SAS Institute, Inc., 1987) and a linearized fit of the log-transformed data, examining the residuals to determine which regression was appropriate. Fish sampled from commercial fisheries were excluded from these analyses because they were eviscerated.

The relation of total length to otolith radius was estimated by regression:

$$L = a + b\,(R),$$

where L = total length in mm; and
R = otolith radius in ocular micrometer units.

Linear regression equations were developed for all data pooled as well as for north Florida and south Florida. Back-calculated size of each fish at the time of formation of each annulus was determined by substituting the measurement to each annulus into a body-proportional equation (Francis, 1990):

$$L_i = \left\{(a + bS_i) / (a + bR)\right\} L,$$

where L_i = fish total length (mm) at annulus i;
R = otolith radius;
a = intercept from the L-R regression;
b = slope from the L-R regression; and
S_i = measurement to the i^{th} annular ring.

Back-calculated size at time of formation of the last annulus was used in order to provide length-at-age data unbiased by differences in time of year of sampling. Area-specific data were developed by substituting coefficients from the area-specific L-R regressions into Francis's (1990) body-proportional equation. Use of a single back-calculation per fish avoids the violation of assumption of independence among sample elements (Vaughan and Burton, 1994), but this method does not necessarily provide all available information about the growth of all cohorts.

Theoretical growth parameters were estimated by fitting the back-calculated lengths at age to the von Bertalanffy (1938) growth equation:

$$L_t = L_\infty \left[1 - \exp\left(-K(t - t_0)\right)\right],$$

where L_t = total length at age t;
L_∞ = theoretical asymptotic length;
K = Brody growth coefficient; and
t_0 = theoretical age when fish length = 0.

Parameter estimates were obtained by using nonlinear regression analysis (SAS Institute, Inc., 1987). Theoretical lengths at age were derived for back-calculated lengths at age by using the last annulus (Vaughan and Burton, 1994).

I estimated the instantaneous rate of natural mortality (M), by area, using several methods. I used Hoenig's (1983) longevity-mortality relationship,

$$\ln(Z) = 1.709 - 1.084 \times \ln(t_{max}),$$

where t_{max} = the maximum age encountered; and estimates of M are for relatively unexploited stocks.

I used a second equation which adjusts for sample size in Hoenig (1983), who reasoned that with a larger sample

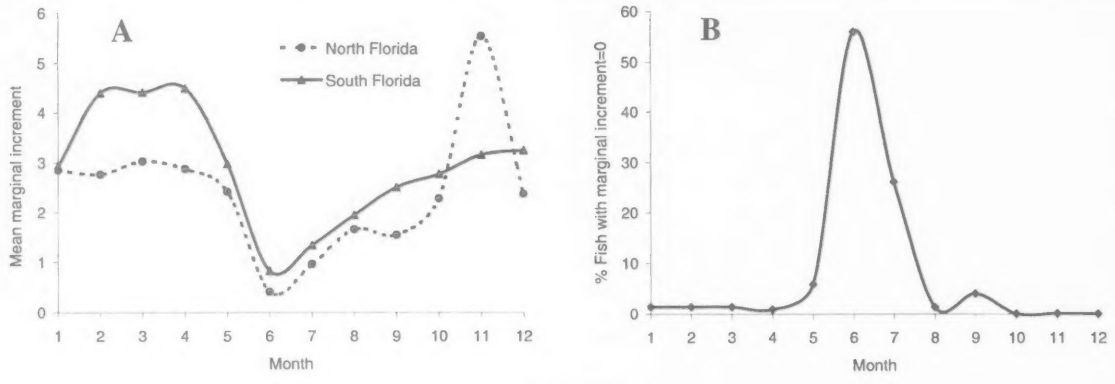

Figure 1

(**A**) Mean monthly marginal increment by area for gray snapper, all ages combined; (**B**) monthly percentage of fish with a marginal increment = 0.

size there is a greater probability of encountering the true maximum age of the fish:

$$Z = \ln (2n + 1)/(t_{max} - t_c),$$

where n = the sample size; and
t_c = the first age fully represented in the catches.

I used the Pauly (1980) method

$$\log_{10}M = 0.0066 - 0.279 \times \log_{10}L_\infty + 0.6543 \times \log_{10}K + 0.4634 \times \log_{10}T,$$

where L_∞ = the asymptotic length;
K = the Brody growth coefficient from the von Bertalanffy (1938) growth equation; and
T = the mean annual seawater temperature (°C).

I derived the latter from sea surface temperature readings from buoys operated by NOAA's National Oceanographic Data Center during 1998. Finally, I estimated M by using the regression of Ralston (1987):

$$M = 0.0189 + 2.06 \times K,$$

where K = the Brody growth coefficient.

Observed ages at length for all years combined were used to develop age-length keys (ALK) for each area (Ricker, 1975). I assigned aged fish (my samples) to 25-mm-TL intervals and calculated age distribution (as a percentage) for each size interval. Area-specific age-length keys were used to convert length frequencies from each area and fishery, weighted by the corresponding annual landings, into age frequencies by assigning ages to unaged fish from the length frequencies. Length-frequency data and annual landings data were acquired from the South Atlantic headboat survey, the MRFSS, and the Trip Interview Program (TIP)[5] survey. Total instantaneous mortality rate, Z, was estimated by the absolute value of the slope of the descending right limb of the plot of $\log_e$ *age frequency* on *age* (catch curves) (Beverton and Holt, 1957). Only fully recruited ages (age groups to the right of the top of the dome of the curve) were used to estimate Z because the age group at the top of the catch dome may not be fully vulnerable to the fishing gear (Everhart et al., 1975).

Results

Age determination and validation of annuli

A total of 98% (1243 of 1260) of gray snapper sampled had legible cross-sectioned otoliths. Opaque rings were distinct and easily counted. Otolith radius was correlated with fish length across all ages:

North Florida:
$TL = (10.02 \times OR) - 52.98$ (r^2=0.90, n=519),
South Florida:
$TL = (9.90 \times OR) - 91.68$ (r^2=0.78, n=724),
Areas combined:
$TL = (11.05 \times OR) - 130.32$ (r^2=0.89, n=1243).

Marginal increment analyses showed one minimum per year in June, validating the annual periodicity of otolith increments (Fig. 1A). The monthly percentage of fish with a marginal increment equal to zero (Fig. 1B) showed a single maximum and provided further evidence that annulus formation occurred yearly in June or July. To satisfy Beamish and McFarlane's (1983) assertion that individual ages need to be validated, I analyzed marginal increments by age for

[5] Trip Interview Program. 1998. Administered by Southeast Fisheries Science Center, NMFS, NOAA, 75 Virginia Beach Dr., Miami, FL 33149.

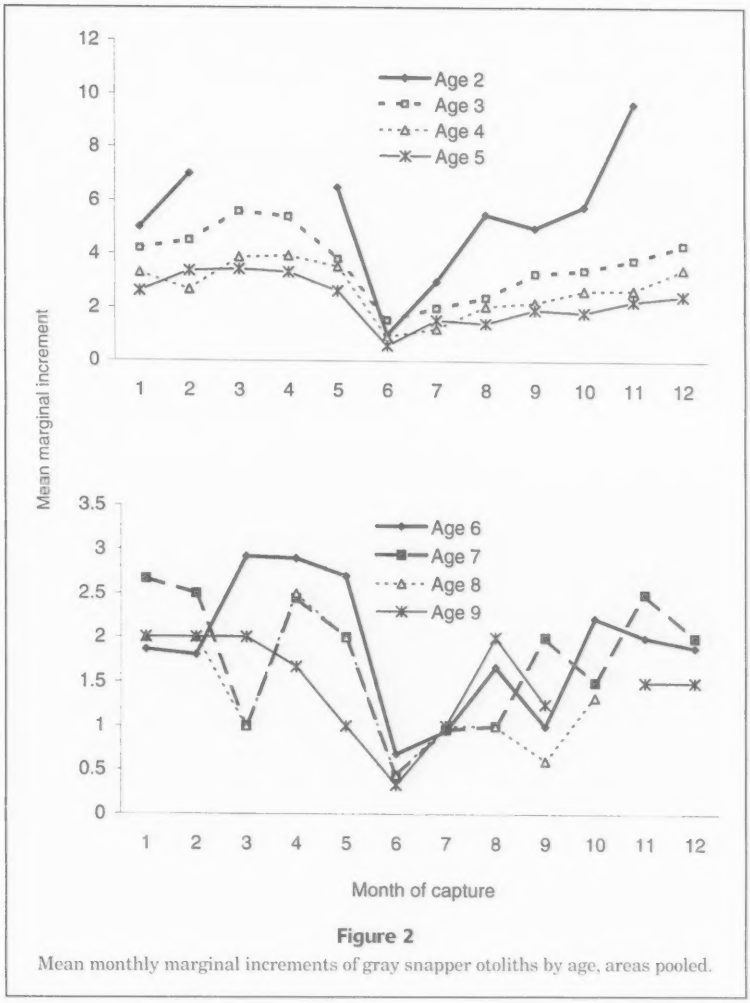

Figure 2
Mean monthly marginal increments of gray snapper otoliths by age, areas pooled.

all areas pooled. Annulus formation occurred in the summer months, with minima in June, for ages 2–9 (Fig. 2). Sample size was inadequate for analyses of older age classes.

Weight-length relationship

The relationship between W (kg) and TL (mm) for all gray snapper measured by the headboat survey from 1982 to 1997 was estimated by using a direct nonlinear fit with SAS PROC NLIN and the Marquardt algorithm software (SAS Institute, Inc., 1987). Examination of the residuals indicated an additive error term, and I concluded that the nonlinear fit was more appropriate than a linearized log-transform fit of the data. Area-specific regressions (see Table 1 for parameters and statistics) were

$$\text{North Florida: } W = 8.4 \times 10^{-9}\, TL^{3.08},$$
$$\text{South Florida: } W = 5.4 \times 10^{-9}\, TL^{3.15}, \text{ and}$$
$$\text{Pooled areas: } W = 7.22 \times 10^{-9}\, TL^{3.11}.$$

In addition, nonlinear regressions by sex, derived from the subset of aging samples for which I had sex information, were

$$\text{Males: } W = 7.13 \times 10^{-9}\, TL^{3.11}, \text{ and}$$
$$\text{Females: } W = 6.95 \times 10^{-9}\, TL^{3.10}.$$

Although regression coefficients were significantly different by area (t=–8.024, P<0.001, df=10,704, and t=8.159, P<0.001, df=10,704 for intercept and slope, respectively), predicted weights for gray snapper at 300 mm, 400 mm, and 500 mm TL from north and south Florida for the respective length-weight regressions were similar: 0.35 vs. 0.34, 0.87 vs. 0.85, and 1.73 vs. 1.71 (kg). This result is likely due to the ability to detect statistically significant differences with an extremely large sample size when the actual differences may be very small and mean little biologically. Regression coefficients by sex were not significantly different, as indicated by overlapping 95% confidence intervals.

Table 1

Parameters and associated statistics for weight-length relationships of gray snapper by area and sex. SE = standard error; MSE = mean squared error.

Parameter (SE)	North Florida	South Florida	Areas pooled	Males	Females
a	8.4×10^{-9}	5.45×10^{-9}	7.22×10^{-9}	7.13×10^{-9}	6.95×10^{-9}
(SE)	(6.25×10^{-10})	(2.76×10^{-10})	$(2.8 \times 10^{\pm 10})$	(1.26×10^{-9})	(1.88×10^{-9})
b	3.08	3.15	3.11	3.106	3.097
(SE)	(0.012)	(0.008)	(0.006)	(0.029)	(0.041)
n	4034	6670	10,704	262	212
MSE	0.078	0.020	0.042	0.019	0.034

Table 2

Mean observed total lengths at age of gray snapper by area.

	North Florida			South Florida		
Age (yr)	n	Mean Tl ±SE (mm)	Range (mm)	n	Mean TL ±SE (mm)	Range (mm)
1	13	218 ±24	181–255	—		
2	7	220 ±24	185–257	20	284 ±36	167–327
3	17	347 ±43	212-415	138	302 ±33	182–397
4	69	388 ±42	307–505	260	325 ±29	231–447
5	138	432 ±42	332–555	177	358 ±45	265–525
6	75	467 ±46	347–565	81	397 ±60	300–644
7	71	525 ±43	370–615	32	474 ±46	390–578
8	26	549 ±40	480–615	11	468 ±60	342–542
9	36	589 ±42	525–702	3	417 ±141	330–581
10	23	595 ±31	537–657	3	414 ±86	317–481
11	14	608 ±32	545–645	1	452	
12	9	623 ±30	580–685	—		
13	8	660 ±35	600–705	2	501 ±166	383–618
14	7	652 ±43	600–725	—		
15	3	682 ±34	660–722	1	504	504–504
16	1	677				
17	1	635				
18	2	649 ±68	600–697			
19	1	707				
20	1	630				
21	2	710 ±25	692–727			
22	—					
23	2	748 ±18	735–760			
24	2	740 ±28	720–760			

Growth

Mean observed lengths at age were larger for fish from north Florida than those for fish from south Florida for all ages except age 2 (Table 2), but sample size may have affected estimates for age-2 fish. North Florida fish ranged from 181 mm at age 1 to 760 mm at age 24. South Florida fish ranged from 167 mm TL at age 2 to 618 mm at age 13. The oldest fish from south Florida was age 15 and measured 504 mm. Age-1 fish were difficult to acquire in south Florida because of minimum-size catch regulations (305 mm TL in federal waters, and 250 mm TL in Florida waters). All age-1 fish from north Florida were collected through fishery-independent hook-and-line sampling. In both areas, most fish attain the federal minimum size limit (305 mm TL) by age 3.

Back-calculated sizes at age of gray snapper by area are shown in Tables 3 and 4. The mean total back-calculated lengths for gray snapper from north Florida, back-calculated to the last annulus, were larger than those for fish from south Florida for all ages except age 2. Given the obvious differences in size at age between the two areas, it seemed inappropriate to pool the data for the purposes of analyzing growth.

The linear regressions of the measurements to the first and second annuli on age for headboat and commercial specimens from north Florida were significantly different from zero (n=519, P=0.0001, r^2=0.04; and n=506, P=0.0012, r^2=0.02). Although this result indicates the presence of Lee's phenomenon for samples from these fisheries (Potts et al., 1998), the model explains very little of the variation, so that Lee's phenomenon was weak and likely masked by other environmental variables. The linear regressions of the measurements to the first and second annuli on age for headboat and commercial specimens from south Florida were not significantly different from zero (n=720, P= 0.23, r^2=0.002 and n=720, P=0.81, r^2=0.0001), indicating that size-selective mortality was not detected.

The von Bertalanffy (1938) growth equations, fitted to back-calculated lengths at age for the last annulus (Fig. 3A), were

North Florida:
$L_t = 717\,(1 - e^{-0.17\,(t\,+\,0.025)})$, and

South Florida:
$L_t = 625\,(1 - e^{-0.13\,(t\,+\,1.33)})$.

Parameters and associated statistics for these equations as well as for equations fitted to the subset of data by sex, are listed in Table 5. Estimates of growth parameters were not significantly different between sexes [Hotelling's T^2 test, $F_{(0.025,3,\infty)}$= 1.0 (Bernard, 1981)] (Fig. 3B). However, estimates of growth parameters were significantly different between areas ($F_{(0.025,3,\infty)}$=84.1).

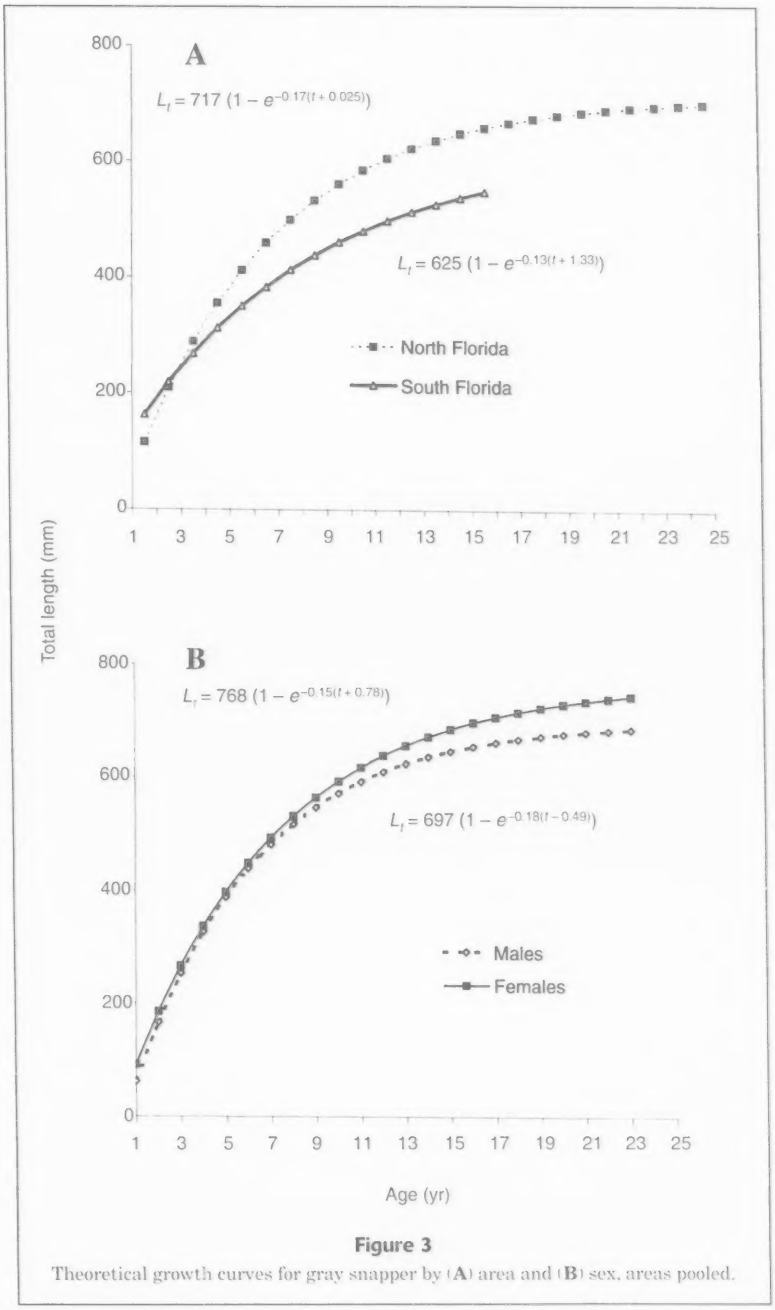

Figure 3
Theoretical growth curves for gray snapper by (**A**) area and (**B**) sex, areas pooled.

Mortality

Estimates of the instantaneous rate of natural mortality (M) varied considerably by method but were similar across areas for a given method. Estimates of M assume a constant natural mortality and so apply to all ages of fish. Hoenig's (1983) longevity-mortality relation returned the lowest estimates, 0.18 and 0.29 (north and south Florida), and his equation adjusted for sample size returned similar values between areas, 0.33 and 0.35. Pauly's (1980) equation, with growth parameters and mean seawater temper-

Table 3

Back-calculated total lengths (mm) of gray snapper aged by sectioned otoliths for North Florida. Obs. age = observed age.

		Annulus number																							
Obs. age	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	13	121																							
2	7	82	166																						
3	17	109	225	307																					
4	69	119	228	304	357																				
5	137	126	247	320	371	412																			
6	74	134	250	318	371	413	450																		
7	68	139	262	336	391	435	474	509																	
8	25	139	2652	335	389	432	468	504	536																
9	36	142	260	337	393	437	477	515	546	576															
10	22	133	244	321	375	422	462	497	527	556	581														
11	14	134	243	324	379	422	461	497	528	555	579	600													
12	9	129	247	324	377	418	457	490	519	547	574	595	614												
13	8	138	267	335	386	429	464	498	531	563	588	609	630	650											
14	7	126	250	325	374	356	418	452	484	511	539	563	582	604	6243	643									
15	3	114	227	300	356	406	456	493	530	559	583	603	623	643	659	676									
16	1	106	264	326	361	387	414	449	493	528	554	572	589	616	633	6514	668								
17	1	105	253	322	374	409	444	470	505	531	548	565	583	592	600	609	618	626							
18	2	164	262	322	364	392	425	453	476	499	523	541	560	579	597	616	625	635	644						
19	1	85	208	302	368	406	443	472	500	538	575	594	613	632	651	660	669	679	688	698					
20	1	115	201	296	344	382	411	439	468	487	506	525	544	554	563	582	592	601	611	620	630				
21	2	143	240	309	355	392	424	456	489	516	539	562	585	608	627	636	645	654	663	673	691	700			
22																									
23	1	120	219	308	388	437	477	507	537	556	576	596	616	636	646	656	666	675	685	695	705	715	725	735	
24	2	125	236	313	380	433	466	500	529	553	572	596	615	630	639	649	658	668	678	687	697	706	716	730	740
No. of calculations		520	507	500	483	414	277	203	135	110	74	52	38	29	21	14	11	10	9	7	6	5	3	3	2
Weighted means		129	246	322	375	421	463	503	531	558	574	591	609	626	633	642	643	650	662	676	685	706	719	732	740
Annual mean growth increment		129	117	76	53	46	42	40	28	27	16	17	18	17	7	9	1	7	12	14	9	21	13	13	8

atures of 25.0°C and 26.1°C for north and south Florida, estimated M at 0.43 and 0.38 for the two areas. The regression method of Ralston (1987) estimated $M = 0.37$ and $M = 0.29$ for north Florida and south Florida, respectively. I used a variety of estimation methods to give the reader a sense of the variation associated with estimating M, a parameter we often know little about but which is a very important variable in stock assessments.

Estimates of total mortality derived from catch curves differed substantially by area (Fig. 4). Estimates of Z for gray snapper from north Florida averaged 0.35 during 1986–97 for all fisheries combined. Gray snapper were fully recruited to the headboat fishery between ages 5 and 6, to the commercial fishery between ages 7 and 8, and to the private recreational fishery between ages 4 and 5. The average value of Z for 1986–97 for gray snapper from south Florida was 0.94, almost three times that of north Florida. Full recruitment occurs between ages 4 and 5 in all fisheries in south Florida.

Discussion

Differences in growth rates and size at age between areas were great enough to argue against pooling the data for growth analysis. However, the pooled data set does provide the opportunity for comparing my results against a previous similar study for the purpose of validating my aging estimates. Back-calculated lengths at age were in close agreement with lengths estimated previously by Manooch and Matheson (1981). Estimated lengths (mm) for ages 1, 5, 10, and 15 with measurements to the last annulus, were 87 vs. 89, 370 vs. 370, 559 vs. 556, and 630 vs 680 (present study vs. previous study). The close agreement in size

Table 4

Back-calculated total lengths (mm) of gray snapper aged by sectioned otoliths for South Florida.

		Annulus number														
Obs. age	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	—															
2	20	100	227													
3	136	89	195	272												
4	258	90	184	253	305											
5	174	94	190	254	303	341										
6	81	97	192	256	305	346	383									
7	32	96	212	283	337	382	424	461								
8	10	99	203	262	313	355	391	422	451							
9	3	71	179	248	286	317	342	367	392	414						
10	3	77	164	210	253	281	311	336	358	380	404					
11	1	70	152	197	243	279	316	343	370	397	425	443				
12	—															
13	2	84	198	244	280	307	335	358	385	408	431	454	473	491		
14	—															
15	1	73	138	213	260	288	307	335	354	382	401	420	438	457	475	495
No. of calculations		721	721	701	565	307	133	52	20	10	7	4	3	3	1	1
Weighted means		92	191	258	306	346	389	432	412	398	414	443	461	480	475	495
Annual mean growth increment		92	99	67	48	40	43	43	(20)	(14)	16	29	18	19	(5)	20

Table 5

Von Bertalanffy growth parameters and associated statistics for gray snapper by area and sex, 1994–1997.

Data set	L_∞	SE (L_∞)	95% CI	K	SE (K)	95% CI	t_0	SE (t_0)	95% CI	n
North Florida	716	11.33	693–738	0.17	0.01	0.16–0.19	–0.001	0.11	–0.22–0.22	520
South Florida	625	56.33	515–736	0.13	0.02	0.08–0.18	–1.33	0.41	–2.12–0.53	721
Males	697	22.93	652–742	0.18	0.017	0.15–0.21	0.49	0.21	0.08–0.89	339
Females	768	35.7	697–838	0.15	0.017	0.1 –0.18	0.16	0.26	–0.36–0.67	272

at age from these two studies, both of which used otoliths and comprised samples from the same geographic area, validates the aging of gray snapper determined in the present study. Back-calculated lengths at age of gray snapper determined from scales by Starck and Schroeder (1970) were generally smaller than those determined from otolith sections, reasons for which are unclear. My samples, as well as those of Manooch and Matheson (1981), were from Florida's east coast, whereas Starck and Schroeder (1970) used fish from only one location in the Florida Keys. A geographic bias may account for the difference in ages between the two studies.

Marginal increment analysis demonstrated that gray snapper ages 2–9 deposit one annulus per year, in June. These ages account for the majority of age classes in the fishery; thus I posit that the critical evaluations stressed by van Oosten (1929) and Beamish and McFarlane (1983) were met. Annual deposition of growth increments on otoliths of gray snapper was not validated by previous investigators and thus was an essential part of my study.

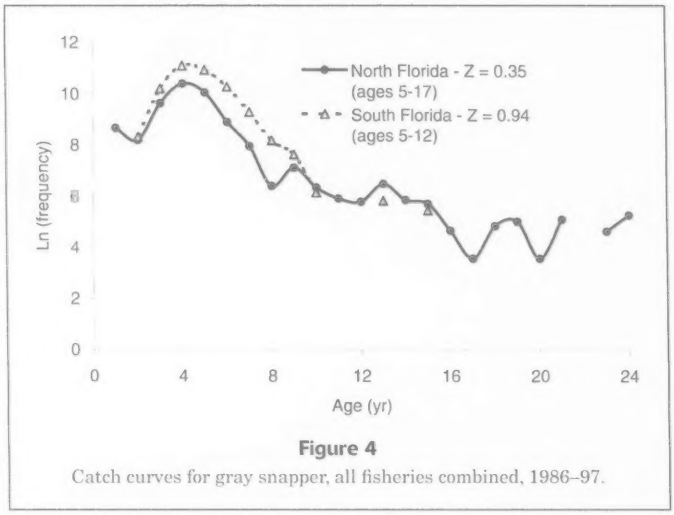

Figure 4

Catch curves for gray snapper, all fisheries combined, 1986–97.

I constructed area-specific age-length keys using Sebastian Inlet, FL (27.8°N latitude), as the north–south dividing line. In addition to being the traditional division point for sample coverage for the south Atlantic headboat survey, it also approximates the nearshore–offshore break in distribution of reef habitat. I did not have enough data to construct annual ALKs as recommended by Ricker (1975) and Westrheim and Ricker (1978), and my decision to produce area-specific ALKs was based on *a priori* information gained as a port agent in Florida from 1982 to 1987. Gray snapper from headboats in north Florida were larger than gray snapper from headboats in south Florida. Moreover, Manooch and Matheson (1981) found differences in length-frequency distributions and estimates of total mortality by area (smaller fish and higher mortality, Z, in south Florida).

The difference in growth of gray snapper between north and south Florida is readily apparent. Mean observed and back-calculated sizes at age were largest for fish from north Florida, and these fish achieved a much greater maximum size and age than did their south Florida counterparts; significant differences in theoretical maximum size between areas were observed (Fig. 3A). Johnson et al. (1994) found similar results for gray snapper collected from the east coast of Florida and the Gulf of Mexico. They compared back-calculated size at age for fish captured from north and south of 27°N latitude and concluded that fish from the northern region were significantly larger than fish from the southern region for ages 1–13. Their latitude was proximal to the headboat survey divisional line used in the present study.

The differences observed in size at age become greater in older ages of gray snapper, although estimates for south Florida are affected by small sample sizes (few fish >age 8). The small sample size of older fish in south Florida probably reflect a lack of abundance rather than sampling deficiencies. Commercial and headboat data (Fig. 5) showed larger and presumably older fish taken from north Florida than from south Florida. The headboat fishery modal length intervals were 400–424 mm TL for north Florida and 300–324 mm TL for south Florida. Modal values of commercial length frequencies showed a greater difference between areas: 550–574 mm TL for north Florida compared with 325–349 TL mm for south Florida. Given the efficiency of modern fishing fleets (all using hook-and-line gear), this finding is strong evidence that the south Florida population of gray snapper has a truncated size distribution. Manooch and Matheson (1981) found a similar disparity in size distribution of gray snapper from headboats from north and south Florida, with respective modes at 450–499 mm TL versus 300–349 mm TL.

One possible explanation for the lack of older, larger fish in south Florida is the much greater fishing pressure there. Manooch and Matheson (1981) estimated the instantaneous rate of fishing mortality (F) to be 0.17 and 0.38 for north and south Florida, respectively. I estimated $F = 0.16$ and $F = 0.66$ for the respective areas for all fisheries combined, using Hoenig's (1983) estimates of $M = 0.18$ and $M = 0.29$ and the area-specific estimates of Z (F=Z–M).

The demography and geography of the Florida peninsula probably affect fishing pressure on gray snapper. South Florida is more densely populated than north Florida and thus has many more potential anglers. Specifically, anglers fished an average total of 186,687 days from south Florida headboats annually from 1982 to 1997, compared with an annual average total of 82,325 days from north Florida headboats. Shorter distance to the fishing grounds in south Florida (5–8 km) than to those in north Florida (40–50 km) also leads to increased exploitation. Increased pressure on younger inshore fish could lead to growth overfishing, whereas easier access to the mature adults offshore may contribute to recruitment overfishing. The

latter scenario would be aggravated by the suspected tendency of gray snapper to undertake spawning migrations to offshore reefs (Domeier et al., 1997). This behavior, resulting in higher fish densities on these reefs, would increase their vulnerability to fishery harvest during summer months, a time of maximum fishing effort due to favorable weather conditions.

Another effect of long-term heavy fishing pressure could be a genetic shift in growth characteristics of the fish. Size-selective mortality could result in slower growing individuals in the population. Buxton (1993) found growth rates for *Chrysolephus cristiceps* (Sparidae) to be significantly lower in exploited than in protected populations. Zhao et al. (1997) found that mean back-calculated lengths at age for vermilion snapper, *Rhomboplites aurorubens*, declined from 1979 to 1987, concluding that this result was a true change in growth, posssibly caused by overfishing. Harris and McGovern (1997) attributed decreases in growth and maturity rates of red porgy (*Pagrus pagrus*), over time, to sustained heavy fishing pressure. Zhao and McGovern (1997) found similar decreases in size and age at maturity for vermilion snapper over time, attributing the declines to increasing fishing pressure. Other investigators, however, have hypothesized that these results were caused by size selectivity characteristics of different gears used during different sampling periods (e.g. Potts et al., 1998).

An alternate explanation for the lack of larger, older gray snapper in south Florida is emigration. An argument might be made that the inshore to offshore spawning migrations (Domeier et al., 1997) previously mentioned might take them beyond the range of the fisheries and make gray snapper less vulnerable to fishing gear in the south Florida area. This hypothesis seems highly unlikely given the range and technology of modern fisheries. Moreover, most reef fishes are thought to exhibit a sedentary lifestyle as adults, staying close to the same general reef area (Ehrlich, 1975; Heemstra and Randall, 1993; Samoilys, 1997). However, Moe (1969) found that red grouper (*Epinephelus morio*) showed some migratory behavior—22 individuals moved 29 km in 50 days, and another individual moved 76 km. Most of these movements were from inshore to offshore. A comprehensive tagging study could be designed to address the question of whether significant numbers of gray snapper migrate out of the south Florida area.

Management of gray snapper is the responsibility of the South Atlantic Fishery Management Council (SAFMC), whose current strategy is to manage this species, and most others in the snapper-grouper complex, as a single stock throughout their management area. It is very unlikely that gray snapper in north and south Florida are genetically distinct because of the northward flow of the Gulf Stream and the resulting widespread distribution of progeny. However, this study in conjunction with that of Manooch and Matheson (1981) strongly suggests that gray snapper have been exploited at higher rates of F in south Florida than in north Florida for at least two decades. As a result, gray snapper reach a smaller maximum size and younger maximum age in the population, as well as smaller sizes at most ages. These biological features carry implications for overall population health because fecundity is usually proportional to size or age, or to both. Fishery managers attempting to assess stocks of gray snapper should perform area-specific analyses in order to manage this species in the most effective manner. Given the results of this study, it seems that managing gray snapper as a stock unit could worsen overfishing conditions in south Florida.

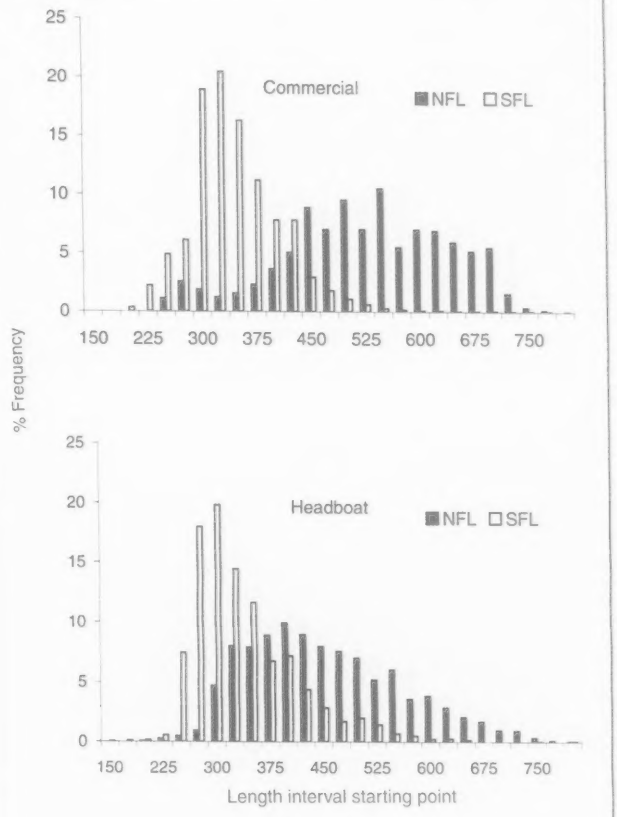

Figure 5

Length frequencies for gray snapper measured by fishery and area, 1986–97.

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Feeding ecology of the Mediterranean spiderfish, *Bathypterois mediterraneus* (Pisces: Chlorophthalmidae), on the western Mediterranean slope

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Abstract–The feeding habits of the Mediterranean spiderfish, *Bathypterois mediterraneus*, the most abundant fish below 1000 m on the deep slope of the Catalan Sea (western Mediterranean), were studied. Samples were obtained at depths between 1000 and 2250 m. Diet was analyzed for two different size classes (immature and mature specimens) and three different bathymetric strata. The most important food items found were benthopelagic planktonic calanoid copepods. In juveniles from 1800 to 2250 m, benthic tanaidaceans were secondary, whereas in the adults, mysids were secondary. At other depths, there were no secondary prey: calanoid copepods were consumed almost exclusively; other items were very scarce. Adults ingest larger amounts and sizes of prey than juveniles. The scarcity of resources below 1200–1400 m diversified the diet, although it still primarily consisted of elements from the benthopelagic plankton.

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The genus *Bathypterois* Günther, 1878 comprises a small group of benthic chlorophthalmid species adapted for life in the deep sea. The genus is circumglobal at temperate latitudes (Sulak, 1984a). Two species of *Bathypterois* are found in the Mediterranean: *Bathypterois dubius* and *Bathypterois mediterraneus* (Bauchot, 1962). The presence of a third, *Bathypterois grallator*, based on underwater photographs, has been suggested by Sulak (1984a). The Mediterranean spiderfish, *Bathypterois mediterraneus*, is the only endemic species of the genus, and undoubtedly the most abundant in the Mediterranean (Sulak, 1977; Bauchot, 1987).

Some species of the genus *Bathypterois*, such as *Bathypterois dubius*, *Bathypterois grallator*, *Bathypterois atricolor*, and *Bathypterois viridensis*, have been observed from submersibles (Church, 1971; Heezen and Hollister, 1971; Saldanha, 1977; Jones and Sulak, 1990; Chave and Mundy, 1994; Chave and Malahoff, 1998). The fish are benthic, rest on the bottom, and touch the sediment with their longest pelvic and caudal rays (Heezen and Hollister, 1971; Saldanha, 1977), while the long pectoral rays are directed forwards over the head (Saldanha, 1977). Pectoral rays are likely used as sensory devices to detect the presence of planktonic prey, by both direct contact and chemoreception (Sulak, 1977).

According to Sulak (1984a), *Bathypterois mediterraneus* is benthic on the continental slope and rise, at 260–2800 m. However, in the Catalan Sea (western Mediterranean), the species is restricted in its bathymetric distribution to depths greater than 748 m (Stefanescu et al., 1992a, 1994; Morales-Nin et al., 1996). Of the 31 different species of deep-water fish in the Catalan Sea (Stefanescu et al., 1992a), *Bathypterois mediterraneus* is subdominant between 1000 and 1500 m, and dominant below this depth. At 1000–2250 m *Bathypterois mediterraneus* is the fourth in importance for biomass of all fish (Stefanescu et al., 1992a). This species aggregates (Stefanescu et al., 1992a; Morales-Nin et al., 1996), contrary to Sulak's (1984a) observation that it is usually solitary, but may aggregate occasionally.

Knowledge of the biology of deep-sea fauna in the Mediterranean is limited. The feeding habits of some deep-water fish and decapod species in the Catalan Sea have been studied recently (Cartes and Sardà, 1989; Carrassón et al., 1992; Cartes and Abelló, 1992; Cartes, 1993a, 1993b, 1993c). Information on *Bathypterois mediterraneus* biology is limited and fragmentary. Data regarding growth and depth-size trends are given by Morales-Nin (1990), Stefanescu et al. (1992b), and Morales-Nin et al. (1996). The morphological and morphometric characteristics of the alimentary tract and some generic data on the diet of this species have been reported by Carrassón and Matallanas (1990, 1994).

Table 1

Sampling data for *Bathypterois mediterraneus* in the present study. N lat = North latitude; E long = East longitude. *n* = number of specimens sampled.

Station	Date	Depth (m) (initial final)	Final situation		
			N lat	E long	*n*
BII-4	Jul 29 1987	1432 1419	40 44.7	1 52.6	2
BII-5	Jul 30 1987	1753 1715	40 25.4	1 56.9	60
BII-6	Jul 31 1987	1287 1329	40 54.7	2 11.5	55
BII-8	Aug 1 1987	1295 1357	41 02.6	2 27.8	59
BIII-3	Jun 25 1988	1774 1783	40 18.5	1 57.2	33
BIII-4	Jun 26 1988	2163 2039	40 37.7	3 06.2	16
BIII-5	Jun 26 1988	2256 2239	40 32.3	3 44.7	80

The object of this paper is to provide new and detailed information on the diet of *Bathypterois mediterraneus* from depths of 1000–2250 m in the western Mediterranean. Its feeding habits are analyzed in different bathymetric strata and within groups of immature and adult specimens. The influence of these factors on diet, and patterns of dietary overlap, are also discussed.

Materials and methods

Samples were collected from the continental slope (1000–2250 m) of the Catalan Sea (western Mediterranean), during two cruises (BATHOS II–III), on board the RV *García del Cid* (Table 1), with a semi-balloon otter-trawl (OTSB14) towed from a single warp (cf. Merret and Marshall, 1981).

All specimens were fixed in 10% formalin immediately after capture. Once in the laboratory, they were measured (standard length: SL, to the nearest millimeter) and dissected to analyze the gut contents. A total of 305 specimens were dissected to examine feeding activity.

The linear and poorly differentiated stomach of *Bathypterois mediterraneus* is almost always found empty; prey are usually found in the intestine. Therefore, intestinal contents were analyzed, which makes identifying prey more difficult, because of advanced digestion.

Food items were identified to the lowest taxonomic level possible. Numbers and weights were registered to the nearest 0.1 mg, after items were dried with blotting paper to remove surface moisture.

The quantitative importance of each prey group in the diet was determined by the index of relative importance (IRI) (Pinkas et al., 1971), defined as

$$IRI = \%F(\%N + \%V),$$

where $\%F$ = frequency of occurrence of the food item;
$\%N$ = numerical percentage of a food item in the stomachs; and
$\%V$ = percentage by volume of the food item in the stomachs (Hureau, 1970).

In our study, weight was used ($\%W$) instead of volume ($\%V$). This modified index has been expressed as $\%IRI = (IRI/\Sigma IRI) \times 100$ (Rosecchi and Nouaze, 1987).

To analyze the diet of *Bathypterois mediterraneus*, individuals from all trawls were grouped according to capture depth (three bathymetric strata: 1000–1425 m; 1425–1800 m; and 1800–2250 m) and size of individuals (two categories: immature or size 1, standard length <113 mm; and mature or size 2, standard length ≥113 mm). The %IRI of the main prey items was determined for each of the six combinations of depth and size by pooling diet data from the individuals included in each combination. The affinity of these six combinations was computed by using a hierarchical analysis (weighted-pair groups methods analysis, WPGMA).

Trophic diversity (H') was calculated, in terms of mean $\%W$ of prey items, by using the Shannon index. Degree of overlap in the diet of *Bathypterois mediterraneus*, by different sizes and bathymetric strata, was determined, based on mean $\%W$ results, by using the quantitative Schoener index (Schoener, 1974).

Results

Of the 305 specimens of *Bathypterois mediterraneus* analyzed, 23 had an empty gut. Forty-nine categories of prey items were identified from the 282 guts containing food (Table 2). Calanoid copepods were the most numerically abundant prey ($\%N$=81.11%), and mysids were the most abundant by mass ($\%W$=37.59%). Calanoid copepods ($\%IRI$=91.63), according to Wishner (1980) and Smith (1982), are planktonic elements of the benthopelagic fauna. Benthic fauna are accidental prey.

From the cluster analysis of the size and depth combinations, we identified four groups (Fig. 1): juveniles collected at depths of 1800–2250 m (group A), adults collected at

this depth (group B), adults and juveniles from other two depth categories (groups C and D).

Group A, juveniles (size 1) from 1800–2250 m

In 68 specimens analyzed, benthopelagic calanoid copepods (Table 2) were the most important prey (*%IRI*=56.26). Benthic tanaidaceans were secondary (Fig. 2A), despite having a low overall weight, because they were frequently captured (*W/specimen*=0.0001 g). Amphipods were the most abundant accidental prey item (*%IRI*=15.27) owing mainly to the weight of *Rhachotropis* sp. and other amphipods (Fig. 2A).

Group B, adults (size 2) from 1800–2250 m

Calanoid copepods predominated in the 25 adult specimens analyzed (*%IRI*=79.52), whereas suprabenthic mysids were secondary because of their high weight (Fig. 2B). Benthic cumaceans were the major accidental prey (*%IRI*=9.6) because of high numerical abundance (Fig. 2B).

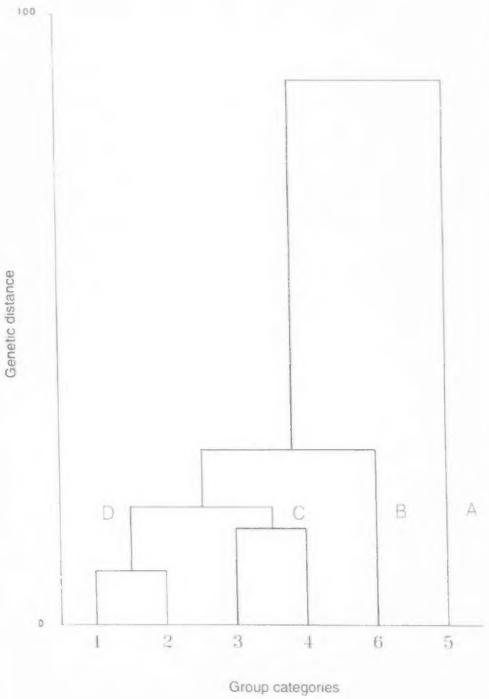

Figure 1

Dendrogram of disimilarity between diets of different groups (bathymetric and ontogenetic) of *Bathypterois mediterraneus*. 1=immature (size 1) individuals of 1000–1425 m depth; 2=mature (size 2) individuals of 1000–1425 m depth; 3=immature (size 1) individuals of 1425–1800 m depth; 4=mature (size 2) individuals of 1425–1800 m depth; 5=immature (size 1) individuals of 1800–2250 m depth; 6=mature (size 2) individuals of 1800–2250 m depth. Groups identified: A = 5; B = 6; C = 3, 4; and D = 1, 2.

Group C, 1425–1800 m

In 95 specimens analyzed, the most important prey were benthopelagic calanoid copepods; their high frequency and abundance (Fig. 3) resulted in a *%IRI* of 95.49%. Incidence of other prey was minimal, *%IRI* <1.5.

Group D, 1000–1425 m

In 94 specimens analyzed, planktonic benthopelagic calanoid copepods were the most important prey (*%IRI*=88.72). Suprabenthic mysids were the major accidental prey because of their high mass (%W=43.11 %) (Fig. 4).

Trophic diversity values (*H'*, Table 2) were lowest at depths of 1425–1800 m, highest in adults from 1800 to 2250 m, and higher in adults than juveniles for all the bathymetric zones analyzed. Dietary overlap (Table 3) was higher between groups 1000–1425 m and 1425–1800 m. Affinity between the diets of juveniles from 1800 to 2250 m and all other groups was low.

Discussion

According to Sulak (1977), *Bathypterois* species feed on benthopelagic plankton. Our study shows that *Bathypterois mediterraneus*, on the deep slope in the Catalan Sea, feed mostly on benthopelagic plankton (calanoid copepods), although occasionally on benthic resources (mainly suprabenthic form; occasionally endobenthic cumaceans, tanaidaceans, etc; or epibenthic amphipods). The long and thin laminar gill rakers of *Bathypterois mediterraneus* (Carrassón and Matallanas, 1994) are highly adapted for retaining planktonic prey and indicate filter feeding. Munk (1965) noted that *Bathypterois* have minute eyes, probably of limited use in feeding. However, Collin and Partridge (1996) suggest that *Bathypterois dubius* may use two retinal area specializations in feeding. *Bathypterois mediterraneus* may exhibit similar behavior. However, there are no photographs of *Bathypterois* with an open mouth that might confirm filter feeding. The small size of *Bathypterois mediterraneus* is important in its feeding because Sulak (1984b) postulated that small-bodied components of the abyssal fauna are microphagous (e.g. *Bathypterois longipes*).

Bathymetric differences were found in the diet of *Bathypterois mediterraneus*. The prey consumed changed with depth, mainly at 1800–2250 m, where juveniles, in addition to benthopelagic calanoid copepods, also fed on endobenthic and epibenthic prey, mostly tanaids (80% of them found in individuals from a catch at a depth of 2250 m). Although a sample taken at 1800 m did not indicate a greater abundance of tanaids than in shallower waters (800–1000 m) (Cartes[1]), it is probable that tanaid abun-

[1] Cartes, J. 1998. Personal commun. Institut Ciències del Mar (CSIC), P. Joan de Borbó s/n, 08039 Barcelona, Spain.

Table 2

Composition of the diet of *Bathypterois mediterraneus* in the four groups (bathymetric and ontogenetic) established. IRI = index of relative importance; %IRI = percentage of IRI. Unid. = unidentified.

	1000–1425 m		1425–1800 m		1800–2250 m			
					Size 1		Size 2	
	(Sizes 1 and 2)		(Sizes 1 and 2)					
Diversity (*H'*)	2.69		2.33		2.87 (2.93)		3.16	
No. of specimens with food	94		95		25		68	
Composition of diet	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI
Foraminifera	—	—	0.3	0.0	—	—	—	—
Polychaeta	75.0	0.6	4.6	0.0	29.4	0.3	42.4	0.3
Polychaeta unid.	41.5	0.4	1.2	0.0	—	—	25.0	0.2
Aphroditimorfa	4.2	0.0	1.1	0.0	29.4	0.3	4.2	0.0
Crustacea								
Crustacea unid.	42.0	0.4	—	—	—	—	—	—
Copepoda	9966.3	77.4	13195.5	90.0	5644.8	52.2	8550.2	67.6
Copepoda unid.	—	—	8.4	0.1	—	—	—	—
Calanoid Copepoda	9966.3	88.7	12531.0	95.5	5014.3	56.3	8550.2	79.5
Harpacticoid Copepoda	—	—	—	—	37.3	0.4	—	—
Ostracoda	20.0	0.2	3.8	0.0	—	—	3.4	0.0
Ostracoda unid.	0.9	0.0	0.1	0.0	—	—	0.4	0.0
Cipridina sp.	—	—	1.0	0.0	—	—	1.5	0.0
Cipridinidae	12.4	0.1	0.4	0.0	—	—	—	—
Amphipoda	609.5	4.7	117.1	0.8	1651.2	15.3	516.5	4.1
Amphipoda unid.	—	—	0.4	0.0	—	—	0.8	0.0
Amphipoda Gammaridea	551.2	4.3	95.2	0.7	1651.2	15.3	477.5	3.8
Amphipoda Gammaridea unid.	138.1	1.2	30.2	0.2	151.8	1.7	122.8	1.1
Orchomene humilis	15.5	0.1	—	—	—	—	—	—
Orchomene sp.	—	—	0.1	0.0	13.6	0.2	—	—
Lyssianasidae	17.8	0.2	3.0	0.0	26.6	0.3	—	—
Harpinia sp.	—	—	1.0	0.0	—	—	—	—
Bruzelia typica	—	—	2.5	0.0	—	—	4.7	0.0
Pseudotiton bouvieri	—	—	—	—	—	—	0.7	0.0
Rhachotropis caeca	0.7	0.0	—	—	—	—	—	—
Rhachotropis sp.	14.7	0.1	—	—	438.3	4.9	30.6	0.3
Monoculodes sp.	0.9	0.0	—	—	—	—	0.9	0.0
Oediceridae	—	—	—	—	—	—	3.9	0.0
Amphipoda Hyperiidea	1.3	0.0	0.2	0.0	—	—	—	—
Isopoda	13.1	0.1	5.0	0.0	22.6	0.2	8.8	0.1
Isopoda unid.	1.3	0.0	2.2	0.0	5.7	0.1	2.9	0.0
Gnathia sp.	1.0	0.0	—	—	—	—	0.4	0.0
Anthuridae	1.0	0.0	0.6	0.0	5.7	0.1	0.3	0.0
Ilyarachna sp.	0.2	0.0	—	—	—	—	—	—
Tanaidacea	0.9	0.0	7.7	0.1	2664.1	24.6	49.5	0.4
Tanaidacea unid.	0.9	0.0	—	—	—	—	—	—
Tanaidae	—	—	7.7	0.1	2664.1	29.9	41.7	0.4
Paratanaidae	—	—	—	—	—	—	0.3	0.0
Cumacea	15.8	0.1	194.6	1.3	751.8	7.0	1214.7	9.6
Cumacea unid.	7.3	0.1	99.3	0.8	401.9	4.5	596.0	5.5
Cyclaspis longicaudata	—	—	0.6	0.0	—	—	14.0	0.1
Leucon longirostris	0.6	0.0	—	—	—	—	—	—
Campylaspis glabra	0.2	0.0	—	—	—	—	—	—
Campylaspis sp.	—	—	0.1	0.0	—	—	—	—

continued

Table 2 (continued)

	1000–1425 m		1425–1800 m		1800–2250 m			
					Size 1		Size 2	
	(Sizes 1 and 2)		(Sizes 1 and 2)					
Diversity (H')	2.69		2.33		2.87 (2.93)		3.16	
No. of specimens with food	94		95		25		68	
Composition of diet	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI
Nannastacidae	—	—	1.6	0.0	—	—	—	—
Platysympus typicus	—	—	2.2	0.0	65.6	0.7	14.7	0.1
Diastylis sp.	—	—	0.2	0.0	7.6	0.1	9.1	0.1
Makrokylindrus sp.	—	—	—	—	—	—	9.4	0.1
Mysidacea	2112.3	16.4	1078.8	7.4	50.3	0.5	2269.5	17.9
Mysidacea unid.	785.5	7.0	196.0	1.5	50.3	0.6	1117.3	10.4
Boreomysis arctica	108.4	1.0	47.0	0.4	—	—	2.2	0.0
Boreomysis sp.	49.3	0.4	148.9	1.1	—	—	198.2	1.8
Parapseudomma sp.	1.2	0.0	—	—	—	—	—	—
Decapoda	4.3	0.0	27.9	0.2	—	—	—	—
Decapoda unid.	4.3	0.0	—	—	—	—	—	—
Larval Decapoda	—	—	0.4	0.0	—	—	—	—
Decapoda Natantia	—	—	17.4	0.1	—	—	—	—
Acanthephyra eximia	—	—	7.2	0.1	—	—	—	—
Pontophilus norvegicus	—	—	1.5	0.0	—	—	—	—
Osteichthyes	—	—	27.0	0.2	—	—	—	—
Scales	16.0	0.1	—	—	—	—	—	—

dance increases in the environment at 2250 m. The mouth position of *Bathypterois* makes it improbable that they can extract tanaids from the substratum, in which these creatures tend to live. Holdich and Jones (1983) observed that some tanaids can swim very fast for short periods and it is probable that *Bathypterois mediterraneus* capture them during these periods. At 1800–2250 m, adult *Bathypterois mediterraneus* consume mysids as secondary prey, which they capture swimming over the bottom.

The scarcity of resources, which decrease even more below 1200–1400 m (Cartes and Sorbe, 1993), may force *Bathypterois* to diversify their diet at 1800–2250 m (H'=2.93), extending to endobenthic prey, such as cumaceans and tanaidaceans. This stenophagic decrease coincides with Dayton and Hessler's (1972) deep predator prototype. Less intense specialization in a type of resource leads deep predators to be more adaptable, whether due to a general scarcity of resources or to the abundance of an occasional single resource.

Ontogenetic differences in the diet were small. Adult intestines mainly contained more and larger prey than did the intestines of juveniles, from all depths. Only at 1800–2250 m were there clear differences in the prey captured by juveniles and adults, possibly reflecting pronounced qualitative changes in the decapod fauna of the western Mediterranean recorded around 2000 m by Cartes (1993d). *Bathypterois grallator*, the largest member of the genus (Sulak, 1977) from the Bahamas, also has an ontogenetic shift in diet (Crabtree et al., 1991), but *Bathypterois longipes* and *Bathypterois phenax* do not significantly shift their diet ontogenetically.

Table 3

Diet overlap (Schoener index) among the different bathymetric and ontogenetic groups established.

	1425–1800 m	1800–2250 m	
	Sizes 1 and 2	Size 1	Size 2
1000–1425 m	0.70	0.50	0.69
1425–1800 m	—	0.47	0.65
1800–2250 m. (size1)	—	—	0.60

Our study goes beyond the preliminary data of Carrassón and Matallanas (1990), indicating that benthopelagic plankton, namely calanoid copepods, play an important dietary role in *Bathypterois mediterraneus*. Further, greater importance for mysids over amphipods (both accidental prey), coincided with their relative abundance in the area (Cartes and Sorbe, 1993). Tanaids were found in the diet for the first time and seem important at depths of 1800–2250 m.

Bathypterois dubius, a related species found in the North Atlantic has a diet broadly similar to that of *Bathypterois mediterraneus* feeding exclusively on planktobenthic copepods (Marshall and Merrett, 1977). However, Sal-

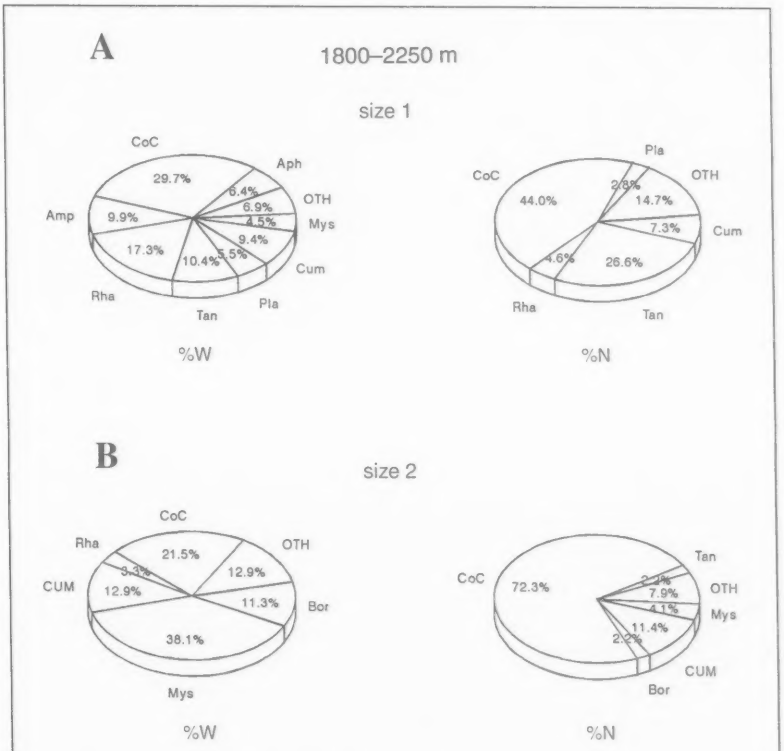

Figure 2

Percentage by weight (*%W*) and by number (*%N*) of prey species in the diet of (**A**) immature (size 1) and (**B**) mature (size 2) individuals at 1800–2250 m depth. CoC = Copepoda Calanoida; Bor = *Boreomysis* sp.; Mys = Mysidacea unidentified.; Pla = *Platysympus typicus*; Cum = Cumacea unidentified.; CUM = total Cumacea; Amp = Amphipoda Gammaridea unidentified.; Rha = *Rhachotropis* sp.; Tan = Tanaidae; Aph = Aphroditimorfa; OTH = Others.

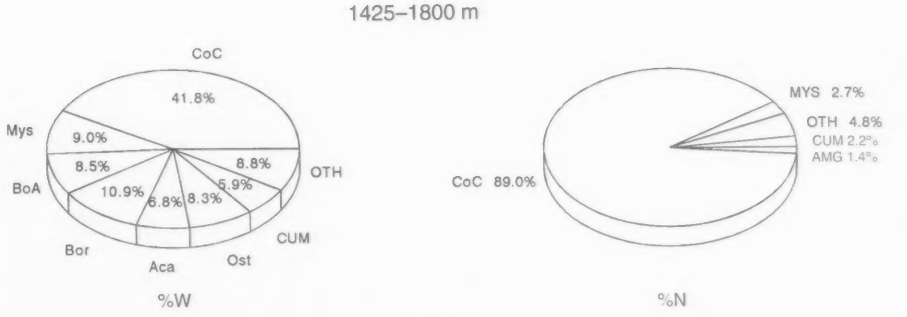

Figure 3

Percentage by weight (*%W*) and by number (*%N*) of prey species in the diet of individuals at 1425–1800 m depth. CoC = Copepoda Calanoida; BoA = *Boreomysis arctica*; Bor = *Boreomysis* sp.; Mys = Mysidacea unidentified.; MYS = total Mysidacea; Aca = *Acanthephira eximia*; Ost = Osteichthyes; CUM = total Cumacea; AMG = total Amphipoda Gammaridea; OTH = Others.

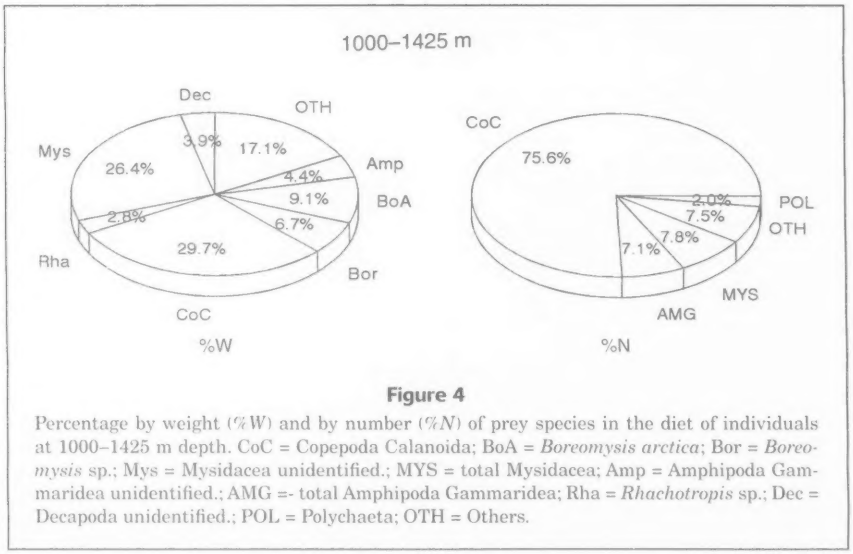

Figure 4

Percentage by weight (*%W*) and by number (*%N*) of prey species in the diet of individuals at 1000–1425 m depth. CoC = Copepoda Calanoida; BoA = *Boreomysis arctica*; Bor = *Boreomysis* sp.; Mys = Mysidacea unidentified.; MYS = total Mysidacea; Amp = Amphipoda Gammaridea unidentified.; AMG =- total Amphipoda Gammaridea; Rha = *Rhachotropis* sp.; Dec = Decapoda unidentified.; POL = Polychaeta; OTH = Others.

danha (1988) reported that *Bathypterois dubius* consumes some amphipods and mysids in addition to calanoid copepods, a finding similar to our data for *Bathypterois mediterraneus*. In the western North Atlantic (Crabtree et al., 1991) and eastern North Atlantic (Marshall and Merret, 1977; Merret, 1987) *Bathypterois longipes* primarily feed on copepods, amphipods, and decapods, but the difference is the greater importance of the benthic prey for *Bathypterois mediterraneus*, especially at depths between 1800 and 2250 m.

In the Atlantic, *Bathypterois dubius* is restricted to depths of less than 2000 m (Sulak, 1984a); *Bathypterois longipes* inhabits depths below 2000 m. Sulak (1977) considered the bathymetric and geographic distribution of these species to be a consequence of competitive interspecific exclusion, and this is supported by the results of Marshall and Merrett (1977). *Bathypterois mediterraneus* is the only abundant Mediterranean species of *Bathypterois*, with a lower bathymetric limit of 2800 m (Bauchot, 1987). In the Catalan Sea, it ranges down to the maximum depth of 2250 m and exclusively exploits a trophic niche unoccupied by any other species. This strategy enables *Bathypterois mediterraneus* to be the dominant species below 1425 m, where resources are more limited.

The relatively higher metabolism as a result of small size in *Bathypterois mediterraneus*, like other *Bathypterois* (Heezen and Hollister, 1971; Saldanha, 1977), is compensated by reduced mobility and coupled with a microphagous filtering diet based on organisms distributed more uniformly in space, such as calanoid copepods. This trophic strategy makes *Bathypterois mediterraneus* especially fit for a nutrient-limited environment, such as the Mediterranean, particularly at greater depths (Carpine, 1970; Thiel, 1983; Pérès, 1985).

Bathypterois species are dominant on the middle and lower slope and in the abyssal depths of oligotrophic regions or similar less productive water masses. Sulak (1984b) and Merrett (1987) have noted the major importance of Chlorophthalmidae in marine fauna of oligotrophic environments. In more productive water masses, species with energetically expensive life history patterns dominate the ichthyofauna. In the Mediterranean, changes in biomass are evident so that the larger and middle-size dominant species between 1000 and 1200 m (*Mora moro, Phycis blennoides, Trachyrhynchus trachyrhynchus,* and *Alepocephalus rostratus*) are progressively replaced at greater depth by other smaller species such as *Bathypterois mediterraneus, Coryphaenoides guentheri,* and *Chalinura mediterranea* (Stefanescu et al., 1993). The relative importance of *Bathypterois mediterraneus* increases as depth increases (Stefanescu et al., 1993), parallel to an increasing scarcity of trophic resources (Cartes, 1991; Cartes and Sorbe, 1993). This species is the most abundant fish of the lower slope assemblage (Morales-Nin et al., 1996) and exemplifies a species adapted to a food scarce environment by energetically conservative feeding strategies.

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Larval development of the kishi velvet shrimp, *Metapenaeopsis dalei* (Rathbun) (Decapoda: Penaeidae), reared in the laboratory

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Abstract–The complete larval development of *Metapenaeopsis dalei* (Rathbun) is described from laboratory-reared larvae. The larvae were reared in a plastic container (20 L). Larvae from the first zoeal stage to the third zoeal stage were fed algae; larvae from the first mysis stage to the first postlarval stage were fed newly hatched nauplii of *Artemia*. The nauplii of *M. dalei* hatched about 20 hours after spawning. The larvae passed through six naupliar, three zoeal, and three mysis stages before the postlarval stage. About 15 days (about 347 hours) were required from hatching to the first postlarval stage. Larval morphology of *M. dalei* is described and compared with those of other *Metapenaeopsis* spp. The first nauplius stage larva of *M. dalei* bears a chitinous conical protuberance on the mediodistal margin of the body. The third protozoeal stage larva has five dorsomedian abdominal spines on the abdomen. The morphological characters of the first postlarva are 43 scaphognathite setae on the maxilla, three scaphocerite spines on the outer margin of antenna, and sternal plate spines: 2,2,0,1,1.

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The kishi velvet shrimp, *Metapenaeopsis dalei* (Rathbun), inhabits coastal waters of Korea (Kim, 1977) and Japan (Kubo, 1949). Of the 26 penaeid genera comprising 215 species, the genus *Metapenaeopsis* is the largest with 76 species (Pérez Farfante and Kensley, 1997). However, studies on the complete larval development of *Metapenaeopsis* spp. are few.

The mysis and postlarval stages of *Metapenaeopsis mogiensis* (Ratbun) and *Metapenaeopsis andamanensis* (Wood-Mason) and postlarval stages of *Metapenaeopsis barbata* (De Haan) have been partially described by Paulinose (1988) from plankton samples. Jackson et al. (1989) reared *Metapenaeopsis palmensis* (Haswell) in the laboratory and described all the larval stages of the species except the naupliar stages. From previous works on Indo-west Pacific penaeid larvae, they also described the important morphological characters for identification. Chong and Sasekumar (1994) studied the larval development of *Metapenaeopsis stridulans* (Alcock) from the egg to the first postlarval stage reared in the laboratory and prepared descriptions of all the larval stages. Ronquillo and Saisho (1997) provided descriptions and illustrative figures of the complete larval development of *M. barbata* and compared the morphological characters of the larval stages with those of several penaeid species.

The purpose of the present study is to describe the larval development of *M. dalei* from the egg to the postlarval stage and to compare its larval development with that of other known *Metapenaeopsis* larvae.

Materials and methods

On 22 August 1996, gravid females of *Metapenaeopsis dalei* were caught by shrimp trawl in Oeyondo, Korea, and transported to the laboratory of the Taean Fish Hatchery, National Fisheries Research and Development Institute, Korea (NFRDI).

Each of them was kept in a 0.5 t container, containing filtered seawater (22.0°C; 32.2‰), until they spawned. On the night of 22 August 1996, a gravid female spawned, and the eggs hatched on the next day. The larvae were reared in a plastic 20-L container. Half the total volume of rearing water was changed daily with fresh seawater (24.0–26.0°C; 32.2–33.2‰). The larvae were fed with a mixture of algae (*Chaetoceros calcitrans* and *Isochrysis galbana*) from the first zoeal stage to the third zoeal stage and with newly hatched nauplii of *Artemia* from the first mysis stage to the first postlarval stage.

For size measurement and morphological observation, eggs were sampled from the bottom of the rearing tank immediately after having been spawned; the developmental processes of the eggs were observed every 10 minutes, the nauplii were sampled at four hour intervals after hatching, and subsequent larval stages were sampled at least twice a day.

The following measurements were taken from preserved larvae by using an ocular micrometer: total length (TL), from the tip of the rostrum to the tip of the caudal end or telson; carapace length (CL), from the anterior margin of

Table 1

Metapenaeopsis dalei. Chronology of embryonic development under laboratory conditions (24.0–26.0°C; 32.2–33.2‰)

Developmental stages	Duration (hour: min.)	Cumulative (hour: min.)
1 cell	00: 23	00: 00
2 cell	00: 25	00: 23
4 cell	00: 26	00: 48
8 cell	00: 28	01: 14
16 cell	00: 20	01: 42
32 cell	00: 28	02: 02
64 cell	00: 50	02: 30
Gastrula stage	04: 50	03: 20
Early embryonic nauplius	05: 30	08: 10
Late embryonic nauplius	06: 30	13: 40
Embryonic nauplius just before hatching		20: 10

Table 2

Metapenaeopsis dalei. Chronology of larval development under laboratory conditions (24.0–26.0°C; 32.2–33.2‰)

Larval stages	Duration (hour)	Cumulative (hour)
First naupliar stage	06	006
Second naupliar stage	07	013
Third naupliar stage	07	020
Fourth naupliar stage	08	028
Fifth naupliar stage	08	036
Sixth naupliar stage	12	048
First protozoeal stage	48	096
Second protozoeal stage	60	156
Third protozoeal stage	50	206
First mysis stage	46	252
Second mysis stage	26	278
Third mysis stage	49	327
First postlarval stage	119	446

the carapace to the midposterior margin of the carapace for zoeae, from the postorbital margin to the midposterior margin of the carapace for mysis and first postlarvae; body width (BW), the greatest width across the body for nauplii.

Results

Development of larvae and duration of the larval stage

A gravid female of *Metapenaeopsis dalei* spawned for two hours from 22:00 to 24:00. The egg was spherical and greenish grey, with a mean diameter of 0.35 mm (n=20). The nauplius hatched about 20 hours after spawning (Table 1). The larvae passed through six naupliar, three zoeal, and three mysis stages, before the postlarval stage. About 15 days (about 347 hours) were required from the hatching to the first postlarval stage (Table 2).

Descriptions of larvae

First naupliar stage (Fig. 1, A and B)

Size TL: 0.37 mm (0.35–0.41 mm; SD=0.02; n=12)
BW: 0.23 mm (0.21–0.25 mm; SD=0.02; n=12)

Body (Fig. 1, A and B): Slightly oval in dorsal or ventral view, convex dorsally; anterodorsal median ocellus; posterior margin rounded; one chitinous conical protuberance on posterodorsal part of body; caudal end with one pair of setae; body unsegmented; three pairs of appendages with naked setae.

Antennule (Fig. 1A): Uniramous; two terminal setae and four lateroventral setae.

Antenna (Fig. 1A): Biramous; endopod with three terminal and two lateroventral setae; exopod with three terminal and three lateroventral setae.

Mandible (Fig. 1A): Biramous; endopod and exopod each with one lateroventral and two terminal setae.

Second naupliar stage (Fig. 1, C and D)

Size TL: 0.43 mm (0.37–0.53 mm; SD=0.04; n=15)
BW: 0.23 mm (0.16–0.27 mm; SD=0.03; n=15)

Body (Fig. 1, C and D): Elongate oval in dorsal or ventral view; anterodorsal median ocellus; posterior margin rounded; posterodorsal protuberance absent; caudal end with two pairs of setae; three pairs of appendages with bipinnate setae; body unsegmented.

Antennule (Fig. 1C): Unchanged.

Antenna (Fig. 1C): Unchanged.

Mandible (Fig. 1C): Unchanged.

Third naupliar stage (Fig. 1, E and F)

Size TL: 0.44 mm (0.42–0.45 mm; SD=0.02; n=6)
BW: 0.24 mm (0.21–0.27 mm; SD=0.03; n=6)

Body (Fig. 1, E and F): Form unchanged; anteroventral median ocellus; posterior margin rounded; caudal end with two pairs of setae; body unsegmented.

Antennule (Fig. 1E): Uniramous; three terminal setae, outermost short and four lateroventral setae.

Antenna (Fig. 1E): Biramous; endopod with three terminal and three lateroventral setae; exopod with three terminal and three lateroventral setae.

Mandible (Fig. 1E): Unchanged.

Fourth naupliar stage (Fig. 2, A and B)

Size TL: 0.43 mm (0.40–0.47 mm; SD=0.03; n=4)
BW: 0.23 mm (0.22–0.24 mm; SD=0.01; n=4)

Body (Fig. 2, A and B): Slightly elongate; anteroventral median ocellus; medial notch dividing posterior end into two symmetrical lobes each with 3+3 setae; thoracic part with some rudimentary segmentation ventrally.

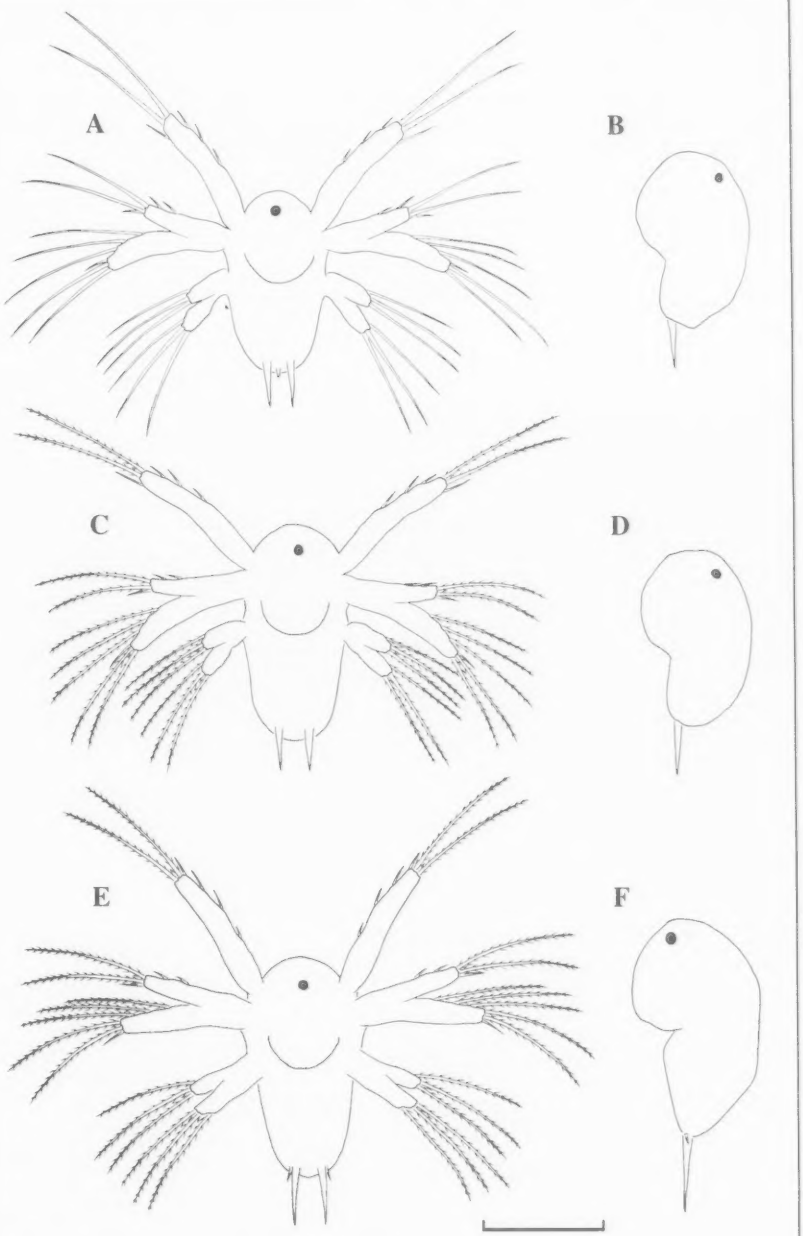

Figure 1

Metapenaeopsis dalei. Nauplius: (**A**) first naupliar stage, ventral view; (**B**) first naupliar stage, lateral view; (**C**) second naupliar stage, ventral view; (**D**) second naupliar stage, lateral view; (**E**) third naupliar stage, ventral view; (**F**) third naupliar stage, lateral view. Scale bar = 0.2 mm.

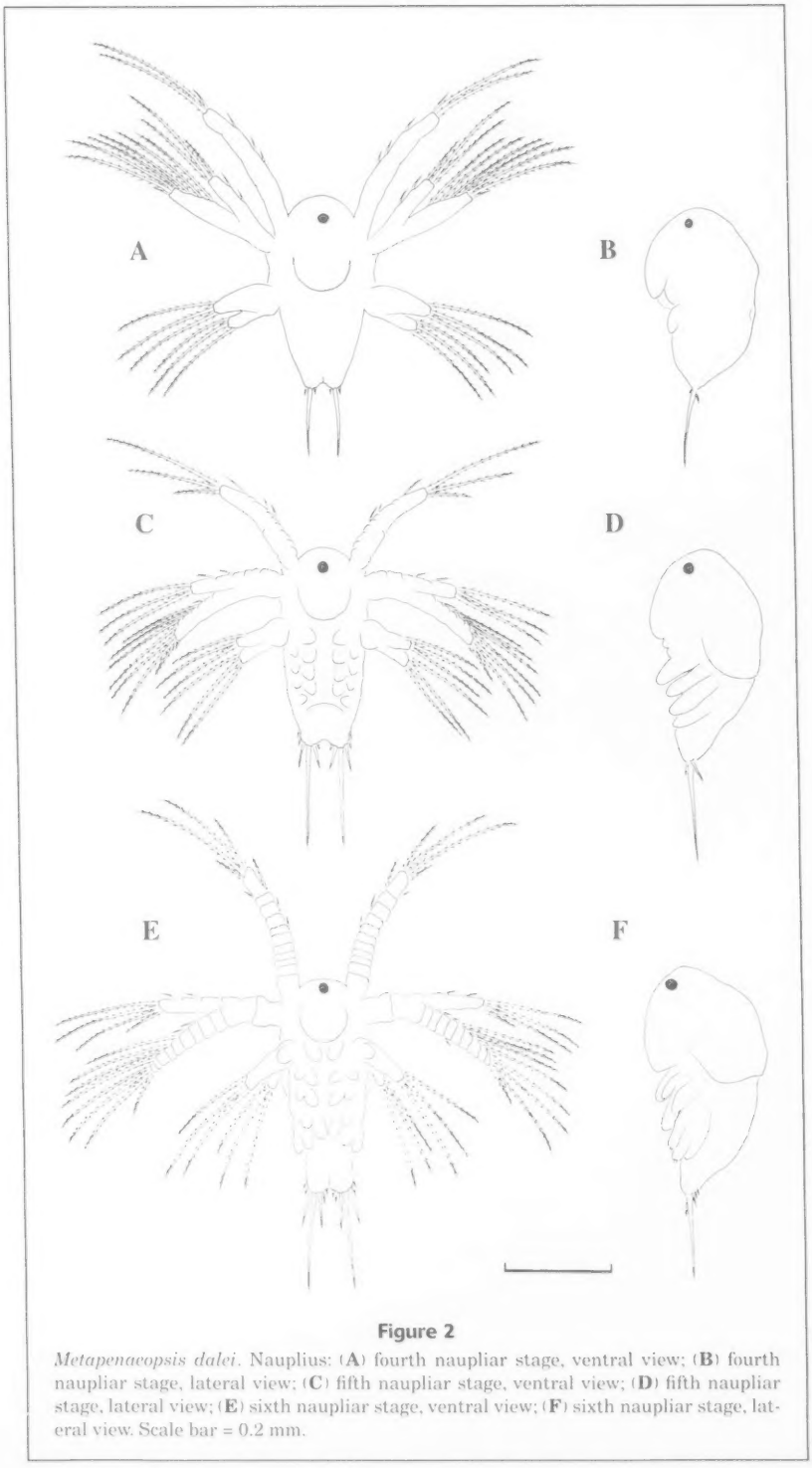

Figure 2

Metapenaeopsis dalei. Nauplius: (**A**) fourth naupliar stage, ventral view; (**B**) fourth naupliar stage, lateral view; (**C**) fifth naupliar stage, ventral view; (**D**) fifth naupliar stage, lateral view; (**E**) sixth naupliar stage, ventral view; (**F**) sixth naupliar stage, lateral view. Scale bar = 0.2 mm.

Antennule (Fig. 2A): Uniramous; three terminal and three lateroventral setae.

Antenna (Fig. 2A): Biramous; endopod with three terminal and two lateroventral setae; exopod with three terminal and four lateroventral setae.

Mandible (Fig. 2A): Biramous; protopodal part swollen; endopod and exopod each with two terminal and one lateroventral setae; coxal part enlarged.

Fifth naupliar stage (Fig. 2, C and D)

Size TL: 0.41 mm (0.34–0.54 mm; SD=0.07; n=10)
BW: 0.18 mm (0.14–0.23 mm; SD=0.03; n=10)

Body (Fig. 2, C and D): Slightly more elongate, tapering towards telson lobes; anteroventral median ocellus; carapace rudimentary; buds of the oral appendages appeared.

Antennule (Fig. 2C): Uniramous; segmentation rudimentary; two terminal and two lateroventral setae.

Antenna (Fig. 2C): Biramous; segmentation rudimentary; endopod with three terminal and two lateroventral setae; exopod with four terminal and five lateroventral setae.

Mandible (Fig. 2C): Biramous; protopod bulbous; setation unchanged.

Telson (Fig. 2C): Bilobed with 6+6 setae.

Sixth naupliar stage (Fig. 2, E and F)

Size TL: 0.56 mm (0.53–0.58 mm; SD=0.01; n=15)
BW: 0.24 mm (0.23–0.26 mm; SD=0.01; n=15)

Body (Fig. 2, E and F): Elongate with distinct waist; anteroventral median ocellus; carapace developed; rudimentary maxillae and maxillipeds bearing numerous short setae.

Antennule (Fig. 2E): Uniramous; 11-segmented with 0, 0, 0, 0, 0, 1, 0, 1, 0, 2, 4 setae.

Antenna (Fig. 2E): Biramous; peduncle two-segmented; endopod four-segmented with 0, 1, 1, 4 setae; exopod 10-segmented with 0, 0, 1, 2, 1, 1, 1, 1, 1, 3/4 setae.

Mandible (Fig. 2E): Unchanged.

Telson (Fig. 2E): Bilobed with 7+7 setae of varying sizes.

First protozoeal stage (Fig. 3, A–I)

Size TL: 1.07 mm (0.97–1.23 mm; SD=0.09; n=10)

Cephalothorax (Fig. 3A): Incompletely and loosely covered by unarmed carapace; carapace round to oval, with shallow posterior median notch, anterior margin with one pair of orbital spines; rostrum absent; paired sessile compound eyes.

Antennule (Fig. 3B): Uniramous; six-segmented with 0, 0, 0, 0, 4, 6 (three aesthetascs) setae.

Antenna (Fig. 3C): Biramous; protopod two-segmented; endopod two-segmented with 5, 5 setae; exopod 10-segmented with 0, 0, 1, 2, 1, 2, 1, 1, 1, 3 setae.

Mandible (Fig. 3D): Endopod and exopod absent; asymmetrical; masticatory surface with lower molar processes and upper curved incisor processes; molar with many small teeth; incisor with 2–4 larger teeth; left and right mandible each with one denticulated tooth.

Maxillule (Fig. 3E): Biramous; protopod two-lobed, coxal endite with eight setae, basal endite with two stout setae and two setae; endopod three-segmented with 3, 2, 5 setae; small exopod with four plumose setae.

Maxilla (Fig. 3F): Biramous; protopod five-lobed, endites with 8, 3, 3, 3, 3 setae; endopod four-segmented with 2, 2, 2, 3 setae; exopod with five plumose setae.

First maxilliped (Fig. 3G): Biramous; protopod partially divided, coxa with six setae, basis with nine setae; endopod four-segmented with 3, 2, 2, 5 setae; exopod with seven plumose setae.

Second maxilliped (Fig. 3H): Biramous; protopod two-segmented, coxa without setae, basis with four setae; endopod four-segmented with 2, 2, 2, 5 setae; exopod with five plumose setae.

Third maxilliped (Fig. 3I): Undeveloped biramous; exopod with two plumose setae.

Post-carapacial region (Fig. 3A): Six thoracic and one free abdominal somites; unsegmented abdomen with forked telson.

Telson (Fig. 3A): Broadly bifurcated in two lobes with seven pairs of plumose setae.

Second protozoeal stage (Fig. 4, A–I)

Size TL: 1.58 mm (1.44–1.83 mm; SD=0.14; n=17)
CL: 0.50 mm (0.40–0.60 mm; SD=0.05; n=17)

Cephalothorax (Fig. 4A): Loosely covered by carapace; carapace armed with long acute rostrum and two pairs of supraorbital spines; rostrum present and exceeding eye; eyes stalked.

Antennule (Fig. 4B): Uniramous; seven-segmented with 0, 0, 0, 0, 1, 4, 6 (three aesthetascs) setae.

Antenna (Fig. 4C): Biramous; protopod two-segmented with 0, 1 setae; unchanged; exopod 10-segmented with 0, 1, 2, 1, 2, 1, 1, 1, 1, 3 setae.

Mandible (Fig. 4D): Form unchanged; left mandible with four denticulate setae; right mandible with one denticulate seta.

Maxillule (Fig. 4E): Biramous; coxal endite with eight setae, basal endite with five stout setae and one seta; endopod three-segmented with 2, 2, 5 setae; exopod with four plumose setae.

Maxilla (Fig. 4F): Biramous; endites with 10, 4, 4, 5, 3 setae; endopod four-segmented with 3, 2, 2, 3 setae; exopod unchanged.

First maxilliped (Fig. 4G): Biramous; coxa with six setae, basis with 12 setae; endopod with 3, 2, 2, 4 setae; exopod unchanged.

Second maxilliped (Fig. 4H): Biramous; coxa with one seta, basis with nine setae; endopod four-segmented with 2, 2, 2, 5 setae; exopod with six plumose setae.

Third maxilliped (Fig. 4I): Undeveloped biramous; exopod with three plumose setae.

Post-carapacial region (Fig. 4A): Six thoracic and six abdominal somites; unsegmented abdomen with forked telson.

Telson (Fig. 4A): Unchanged.

Third protozoeal stage (Fig. 5, A–K)

Size TL: 2.22 mm (1.80–2.43 mm; SD=0.18; n=11)
CL: 0.60 mm (0.50–0.70 mm; SD=0.06; n=11)

Cephalothorax (Fig. 5A): Incompletely covered by carapace; carapace armed with long rostrum and two pairs of supraorbital spines; rostrum long.

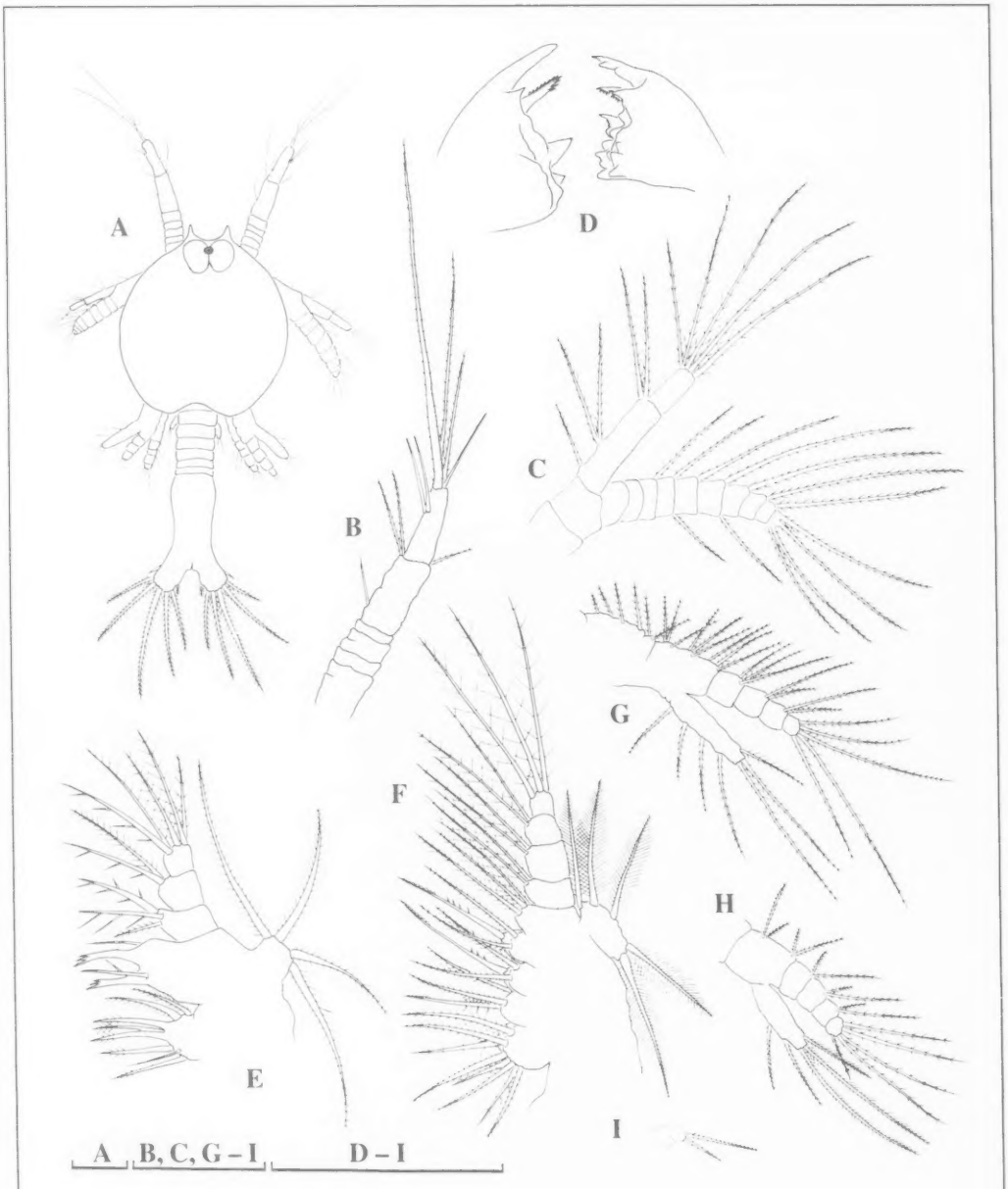

Figure 3

Metapenaeopsis dalei. First zoeal stage: (**A**) dorsal view; (**B**) antennule; (**C**) antenna; (**D**) mandible; (**E**) maxillule; (**F**) maxilla; (**G**) first maxilliped; (**H**) second maxilliped; (**I**) third maxilliped. Scale bars = 0.2 mm.

Antennule (Fig. 5B): Uniramous; four-segmented with 1, 1, 2, 8 (three aesthetascs).

Antenna (Fig. 5C): Unchanged.

Mandible (Fig. 5D): Left mandible with six denticulate setae; right mandible with two denticulate setae.

Maxillule (Fig. 5E): Biramous; coxal endite with eight setae, basal endite with seven stout setae and three setae;

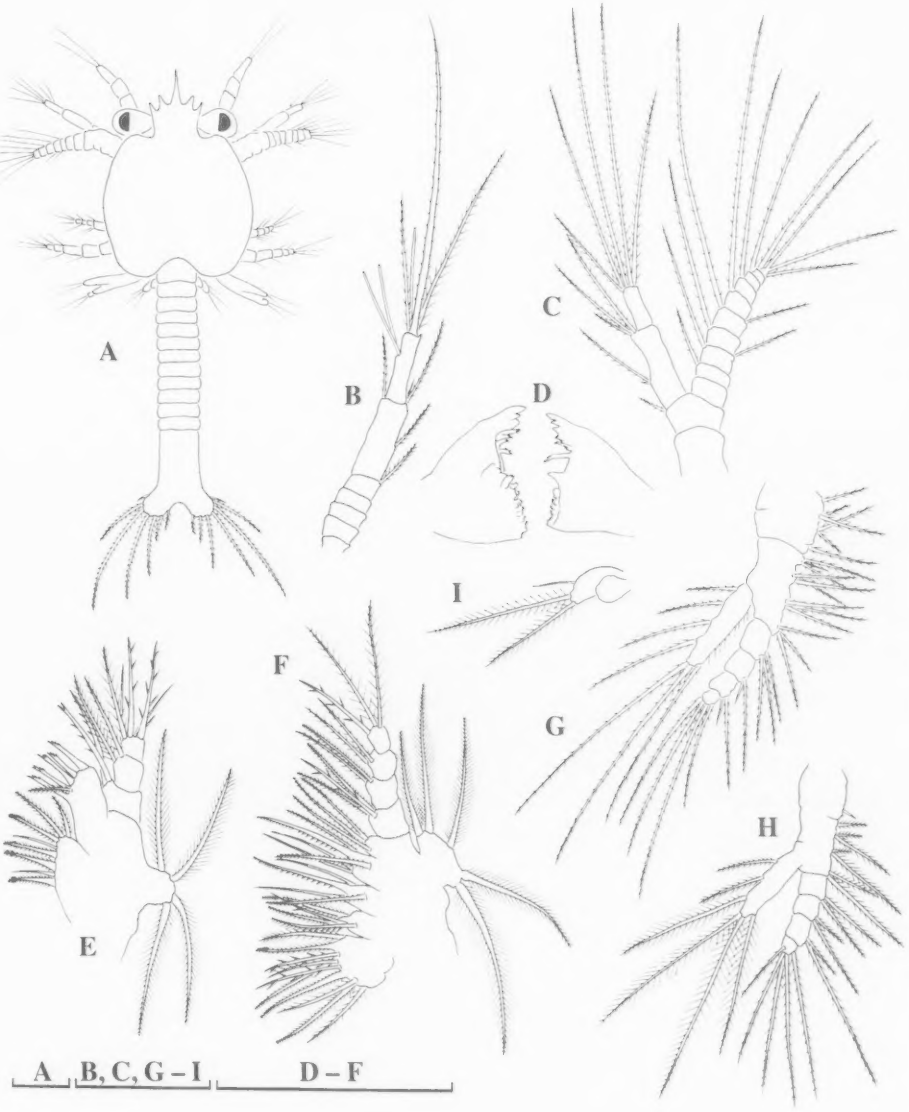

Figure 4

Metapenaeopsis dalei. Second protozoeal stage: (**A**) dorsal view; (**B**) antennule; (**C**) antenna; (**D**) mandible; (**E**) maxillule; (**F**) maxilla; (**G**) first maxilliped; (**H**) second maxilliped; (**I**) third maxilliped. Scale bars = 0.2 mm.

endopod three-segmented with 3, 2, 5 setae; exopod with four plumose setae.

Maxilla (Fig. 5F): Biramous; endites with 11, 5, 6, 6, 4 setae; endopod four-segmented with 3, 2, 2, 3 setae; exopod unchanged.

First maxilliped (Fig. 5G): Biramous; coxa with two setae, basis with seven setae; endopod four-segmented with 3, 2, 2, 5 setae; exopod with nine plumose setae.

Second maxilliped (Fig. 5H): Biramous; coxa with 11 setae, basis with nine setae; endopod four-segmented with 3, 2, 2, 5 setae; exopod with eight plumose setae.

Third maxilliped (Fig. 5I): Biramous; protopod two-segmented, endopod and exopod elongate; endopod with three and exopod with four plumose setae.

Pereiopod (Fig. 5J): Rudimentary and biramous; protopod present.

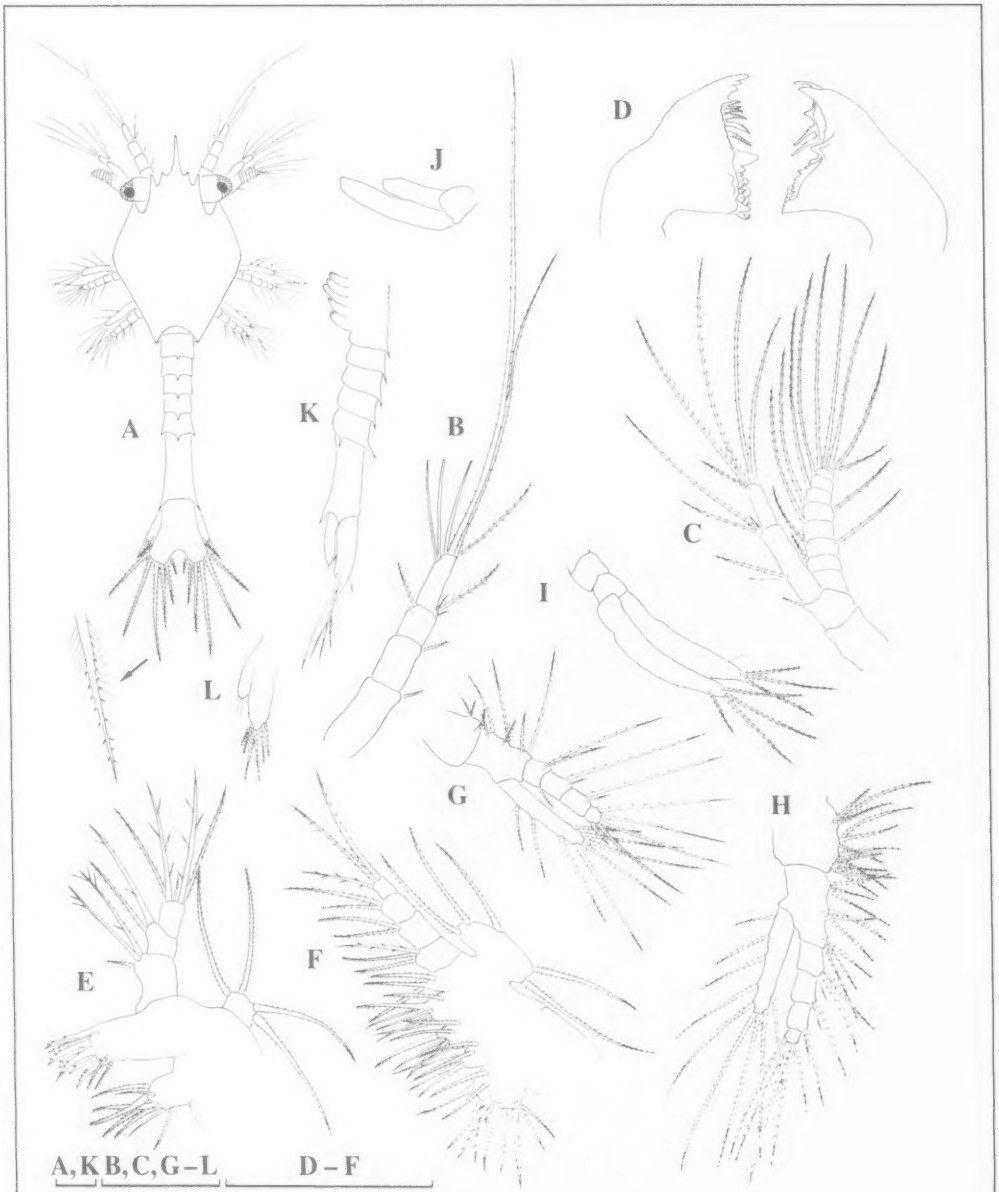

Figure 5

Metapenaeopsis dalei. Third protozoeal stage: (**A**) dorsal view; (**B**) antennule; (**C**) antenna; (**D**) mandible; (**E**) maxillule; (**F**) maxilla; (**G**) first maxilliped; (**H**) second maxilliped; (**I**) third maxilliped; (**J**) pereiopod; (**K**) lateral view of abdomen; (**L**) uropod. Scale bars = 0.2 mm.

Postcarapacial region (Fig. 5, A and K): Abdomen six-segmented; dorsomedian spines on posterior margin of the 1st-5th abdominal somites; one pair of spines on posterolateral margins of 5th and 6th abdominal somites; 6th abdominal somite also with one pair of spines on lateroventral margin; pereiopods appeared.

Uropod (Fig. 5L): Biramous; endopod with three setae; exopod with six setae.

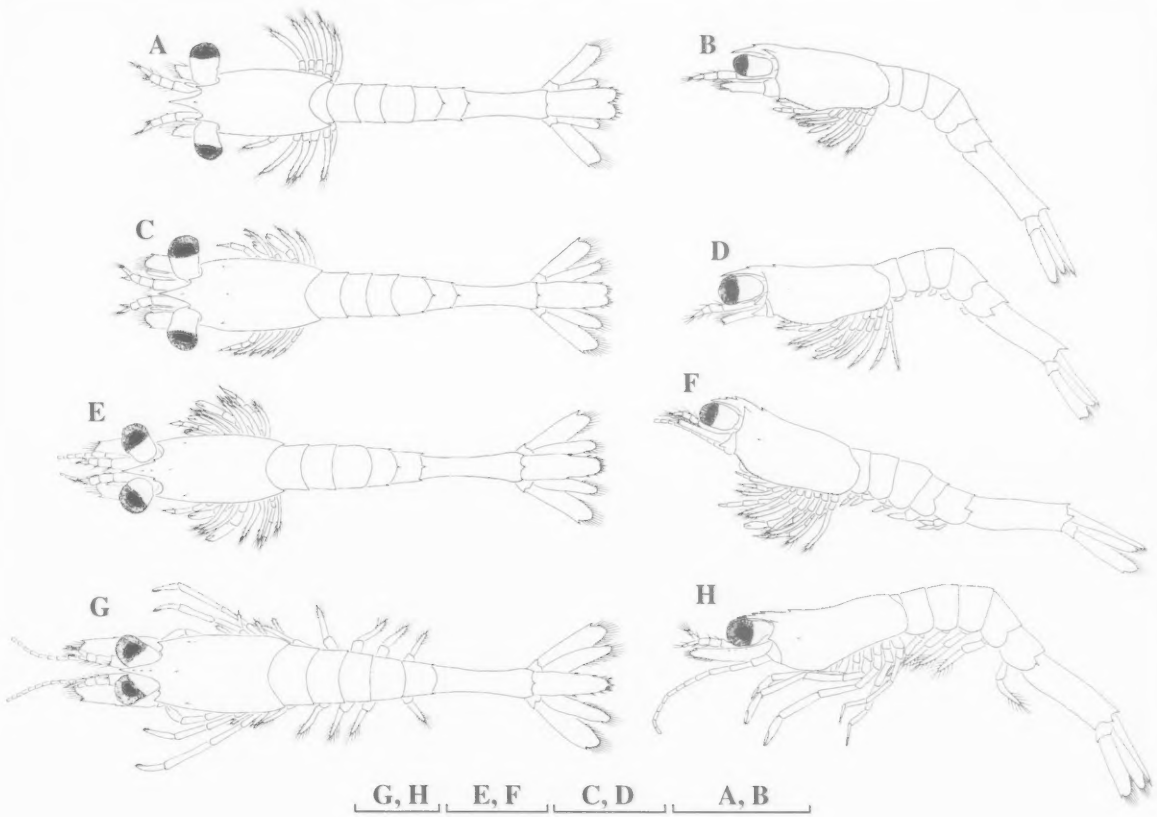

Figure 6

Metapenaeopsis dalei. Mysis and postlarva: (**A**) first mysis stage, dorsal view; (**B**) first mysis stage, lateral view; (**C**) second mysis stage, dorsal view; (**D**) second mysis stage, lateral view; (**E**) third mysis stage, dorsal view; (**F**) third mysis stage, lateral view; (**G**) first postlarval stage, dorsal view; (**H**) first postlarval stage, lateral view. Scale bars = 0.5 mm.

Telson (Fig. 5A): Separated from the 6th abdominal somite with seven pairs of setae.

First mysis stage (Fig. 6, A and B, Fig. 7, A–N)

Size TL: 2.79 mm (2.69–3.07 mm; SD=0.14; n=15)
CL: 0.75 mm (0.64–0.86 mm; SD=0.06; n=15)

Carapace (Fig. 6, A and B): Closely covering thoracic somites; one pair of supraorbital, antennal and pterygostomial spines, 10 anteroventral and three posteroventral spines on each marginal side; rostrum long with one dorsomedian rostral tooth.

Antennule (Fig. 7A): Uniramous; peduncle three-segmented, 1st segment with one large ventral spine, one small proximal spine and 11 setae, 2nd segment with 10 setae, 3rd segment with seven setae; outer ramus with seven aesthetascs; inner ramus with two setae.

Antenna (Fig. 7B): Biramous; protopod two-segmented; endopod and exopod unsegmented; endopod with three naked setae; exopod (scaphocerite) with 12 marginal plumose setae.

Mandible (Fig. 7C): Left mandible with seven denticulate setae; right mandible with three denticulate setae; mandibular palp present as bud.

Maxillule (Fig. 7D): Biramous; protopod two-lobed, coxal endite with eight setae, basal endite with nine stout setae and three setae; endopod three-segmented with 3, 2, 5 setae; exopod with four plumose setae.

Maxilla (Fig. 7E): Biramous; protopod five-lobed, endites with 11, 5, 7, 7, 3 setae; endopod 4-segmented with 2, 2, 2, 3 setae; exopod (scaphognathite) with nine plumose setae.

First maxilliped (Fig. 7F): Biramous; coxa with eight setae, basis with 14 setae; endopod four-segmented with 4, 2, 2, 5 setae; exopod with nine plumose setae.

Second maxilliped (Fig. 7G): Biramous; coxa with three setae, basis with eight setae; endopod four-segmented with 4, 4, 2, 5 setae; exopod with four plumose setae.

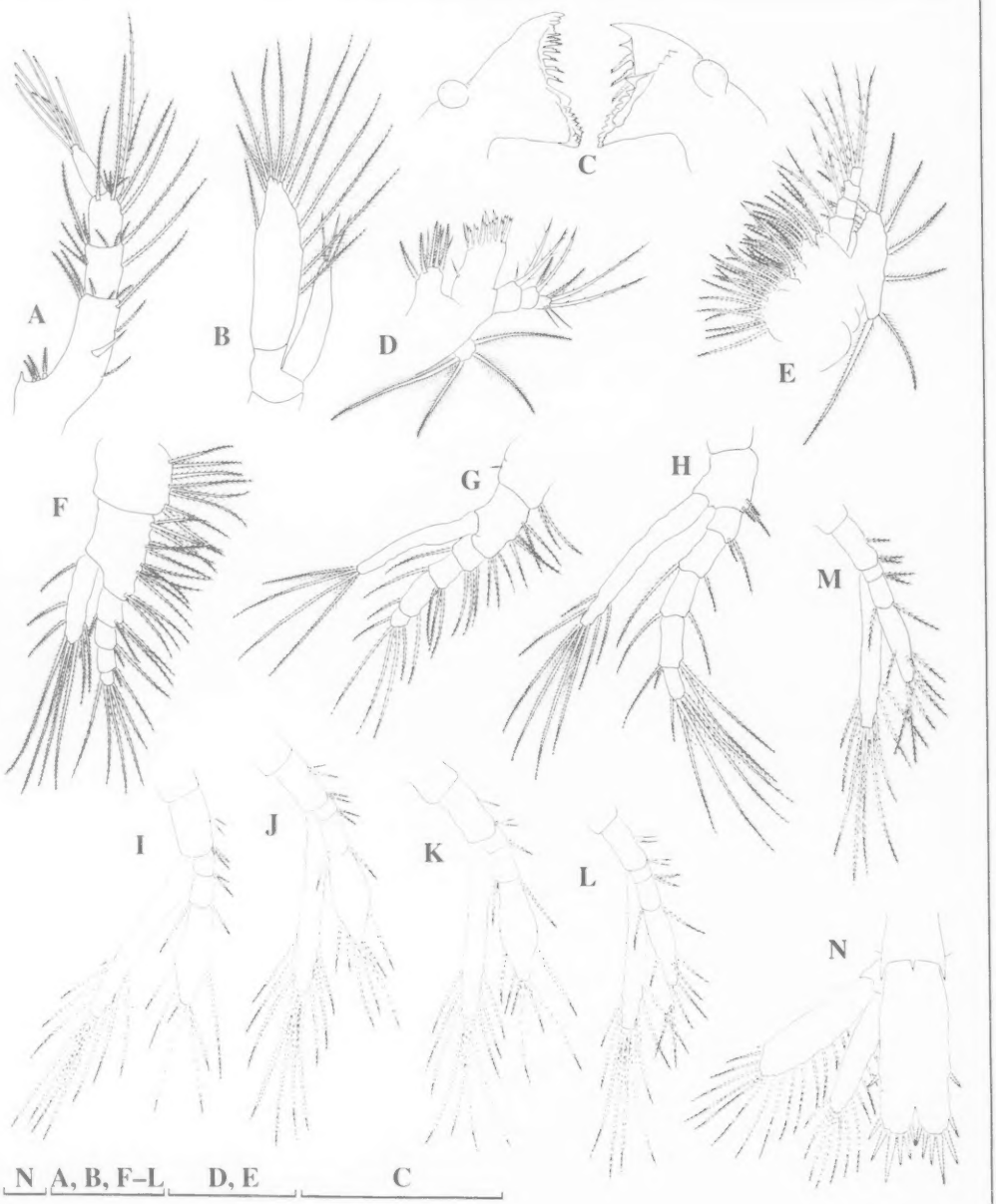

Figure 7

Metapenaeopsis dalei. First mysis stage: (**A**) antennule; (**B**) antenna; (**C**) mandible; (**D**) maxillule; (**E**) maxilla; (**F**) first maxilliped; (**G**) second maxilliped; (**H**) third maxilliped; (**I**) first pereiopod; (**J**) second pereiopod; (**K**) third pereiopod; (**L**) fourth pereiopod; (**M**) fifth pereiopod; (**N**) telson and uropod. Scale bars = 0.2 mm.

Third maxilliped (Fig. 7H): Biramous; coxa naked, basis with three setae; endopod five-segmented with 2, 2, 2, 4, 5 setae; exopod with eight plumose setae.

First pereiopod (Fig. 7I): Biramous; coxa naked, basis with four setae; endopod three-segmented with 2, 2, 7 setae; exopod with 10–11 plumose setae.

Second pereiopod (Fig. 7J): Biramous; coxa naked, basis with four setae; endopod three-segmented with 2, 2, 7 setae; exopod with 10 plumose setae.

Third pereiopod (Fig. 7K): Biramous; coxa naked, basis with three setae; endopod three-segmented with 2, 2, 7 setae; exopod with 10 plumose setae.

Fourth pereiopod (Fig. 7L): Biramous; coxa naked, basis with four setae; endopod three-segmented with 2, 2, 7 setae; exopod with nine plumose setae.

Fifth pereiopod (Fig. 7M): Biramous; coxa naked, basis with three setae; endopod three-segmented with 2, 2, 7 setae; exopod with nine plumose setae.

Abdomen (Fig. 6, A and B): Dorsomedian spines on the 4th, 5th and 6th abdominal somites; one pair of lateral spines on 5th and 6th abdominal somites; one pair of lateroventral spines on the 6th abdominal somite.

Uropod (Fig. 7N): Protopod with one spine; endopod with 11 marginal plumose setae; exopod with one marginal spine and 13–15 marginal plumose setae.

Telson (Fig. 7N): Narrow and deep median notch with seven pairs of setae and one pair of plumose setae.

Second mysis stage (Fig. 6, C and D; Fig. 8, A–O)

Size TL: 3.71 mm (3.16–4.54 mm; SD=0.29; n=19)
CL: 0.87 mm (0.69–1.10 mm; SD=0.09; n=19)

Carapace (Fig. 6, C and D): Covering thoracic somites; one pair of supraorbital, antennal, pterygostomial, and hepatic spines, 10 anteroventral and three ventroposteror spines on each marginal side; rostrum long with one dorsal tooth.

Antennule (Fig. 8A): Uniramous; peduncle three-segmented, 1st segment with one large ventral spine, one small proximal seta and 14 setae, 2nd segment with eight setae, 3rd segment with three setae; outer and inner ramus unchanged.

Antenna (Fig. 8B): Biramous; protopod two-segmented, 2nd segment with one basial spine; endopod three-segmented with 0, 0, 2 setae; scaphocerite with 19 marginal plumose setae.

Mandible (Fig. 8C): Left mandible with three denticulate setae; right mandible with seven denticulate setae; mandibular palp unsegmented.

Maxillule (Fig. 8D): Biramous; coxal endite with six plumed and two naked setae, basial endite with six stout setae and three setae; endopod unchanged; exopod absent.

Maxilla (Fig. 8E): Biramous; endites with 15, 5, 7, 7, 3 setae; endopod four-segmented with 2, 2, 2, 3 setae; scaphognathite with 16 plumose setae.

First maxilliped (Fig. 8F): Biramous; coxa with eight setae, basis with 15 setae; endopod four-segmented with 4, 3, 2, 5 setae; exopod with nine plumose setae.

Second maxilliped (Fig. 8G): Biramous; coxa with two setae, basis with 10 setae; endopod five-segmented with 4, 5, 1, 2, 6 setae; exopod with six plumose setae.

Third maxilliped (Fig. 8H): Biramous; coxa naked, basis with two setae; endopod five-segmented with 2, 3, 3, 3, 4–5 setae; exopod with 8–9 plumose setae.

First pereiopod (Fig. 8I): Biramous; endopod chelate; coxa naked, basis with two setae; endopod five-segmented with 1, 2, 2, 4, 2 setae; exopod with 10 plumose setae.

Second pereiopod (Fig. 8J): Biramous; endopod chelate; coxa naked, basis with one seta; endopod five-segmented with 2, 3, 3, 3, 3 setae; exopod with 10 plumose setae.

Third pereiopod (Fig. 8K): Similar to 1st pereiopod.

Fourth pereiopod (Fig. 8L): Coxa naked, basis with three setae; endopod five-segmented with 2, 3, 3, 5, 2 setae; exopod with 9–10 plumose setae.

Fifth pereiopod (Fig. 8M): Similar to 4th pereiopod.

Abdomen (Fig. 6C, D): Similar to 1st mysis stage.

Pleopods (Fig. 8N): Two-segmented and uniramous, without setae.

Uropod (Fig. 8O): Biramous; protopod with one spine; endopod with 14 plumose setae; exopod with one fused spine and 19 plumose setae.

Telson (Fig. 8O): Median notch less deep with seven pairs of plumose setae and one posteromedian spine.

Third mysis stage (Fig. 6, E and F; Fig. 9 A–J; Fig 10, A–E)

Size TL: 4.45 mm (3.99–4.88 mm; SD=0.25; n=20)
CL: 1.13 mm (0.96–1.31 mm; SD=0.10; n=20)

Carapace (Fig. 6, E and F): Covering thoracic somites; one pair of supraorbital, antennal, pterygostomial and hepatic spines, 10 anteroventral and three posteroventral spines on each marginal side; rostrum long with two dorsal teeth.

Antennule (Fig. 9A): Uniramous; peduncle three-segmented: 1st segment with one large ventral spine, one small proximal spine, 27 plumose setae and statocyst; 2nd segment with 12 plumose setae; 3rd segment with seven plumose setae; outer ramus with eight aesthetascs; inner ramus unchanged.

Antenna (Fig. 9B): Biramous; protopod unsegmented with one spine; endopod nine-segmented, 1st segment with one spine; scaphocerite with 22 plumose setae and one spine.

Mandible (Fig. 9C): Left mandible with seven denticulate setae; right mandible with three denticulate setae; mandibular palp bud present.

Maxillule (Fig. 9D): Biramous; coxal endite with eight setae, basial endite with eight stout setae and three setae; endopod three-segmented with 2, 2, 5 setae.

Maxilla (Fig. 9E): Biramous; endites with 11, 5, 8, 8, 4 setae; endopod four-segmented with 3, 1, 2, 3 setae; scaphognathite with 24 plumose setae.

First maxilliped (Fig. 9F): Biramous; coxa with 10 setae, basis with 18 setae; endopod four-segmented with 4, 2, 4, 5 setae; exopod with 10 plumose setae.

Second maxilliped (Fig. 9G): Biramous; coxa naked, basis with eight setae; endopod five-segmented with 4, 5, 2, 2, 5 setae; exopod unchanged.

Third maxilliped (Fig. 9H): Biramous; coxa naked, basis with two setae; endopod five-segmented with 2, 3, 3, 3, 5 setae; exopod with nine plumose setae.

First pereiopod (Fig. 10A): Biramous; coxa naked, basis with three setae; endopod five-segmented with 2, 3, 2, 4, 2 setae; exopod unchanged.

Second pereiopod (Fig. 10B): Similar to 1st pereiopod.

Third pereiopod (Fig. 10C): Similar to 1st pereiopod.

Fourth pereiopod (Fig. 10D): Biramous; coxa naked, basis with two setae; endopod five-segmented with 2, 2, 2, 4, 2 setae; exopod with 10 plumose setae.

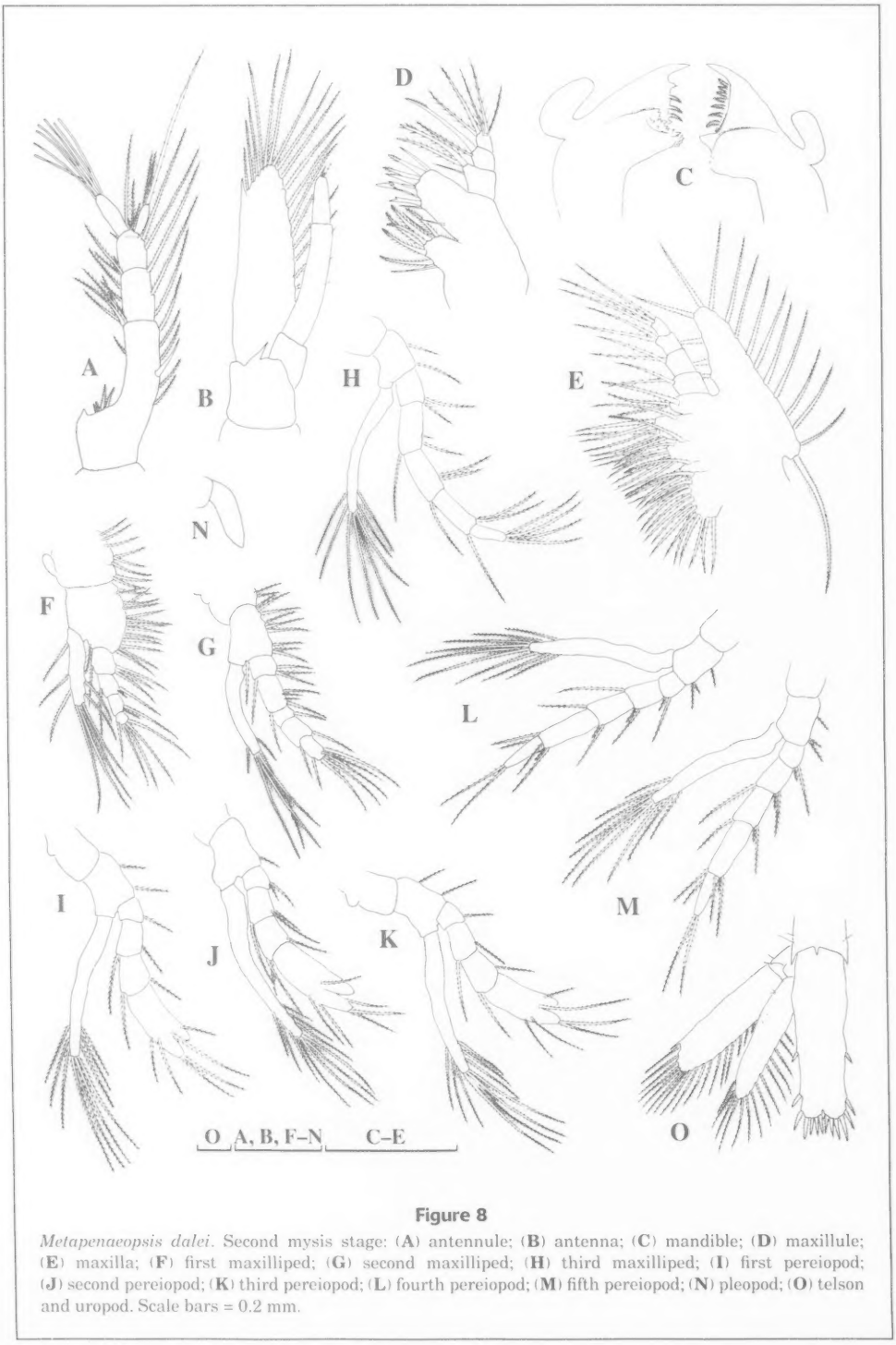

Figure 8

Metapenaeopsis dalei. Second mysis stage: (**A**) antennule; (**B**) antenna; (**C**) mandible; (**D**) maxillule; (**E**) maxilla; (**F**) first maxilliped; (**G**) second maxilliped; (**H**) third maxilliped; (**I**) first pereiopod; (**J**) second pereiopod; (**K**) third pereiopod; (**L**) fourth pereiopod; (**M**) fifth pereiopod; (**N**) pleopod; (**O**) telson and uropod. Scale bars = 0.2 mm.

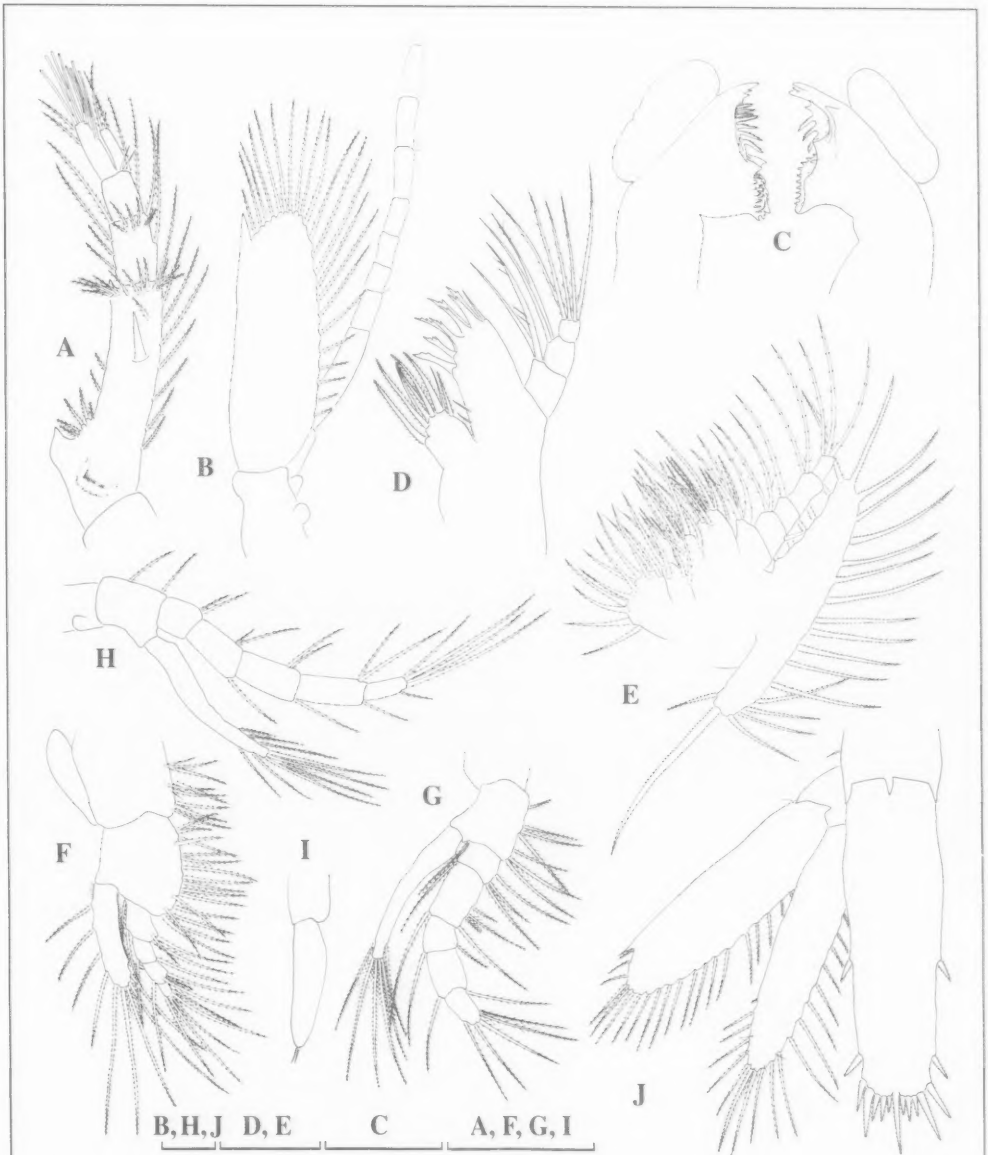

Figure 9

Metapenaeopsis dalei. Third mysis stage: (**A**) antennule; (**B**) antenna; (**C**) mandible; (**D**) maxillule; (**E**) maxilla; (**F**) first maxilliped; (**G**) second maxilliped; (**H**) third maxilliped; (**I**) pleopod; (**J**) telson and uropod. Scale bars = 0.2 mm.

Fifth pereiopod (Fig. 10E): Similar to 4th pereiopod.

Abdomen (Fig. 6F): Similar to 2nd mysis stage.

Pleopods (Fig. 9I): Two-segmented with 0, 2 minute terminal setae.

Uropod (Fig. 9J): Protopod with one spine; endopod with 19 plumose setae; exopod with one fused spine and 20 plumose setae.

Telson (Fig. 9J): Posterior margin straight, with seven pairs of plumose setae and one posteromedian spine.

First postlarval stage (Fig. 6 , G and H; Fig. 11, A–J; Fig. 12, A–J)

Size TL: 5.07 mm (4.68–5.64 mm; SD=0.31; n=20)
CL: 1.21 mm (1.03–1.51 mm; SD=0.14; n= 20)

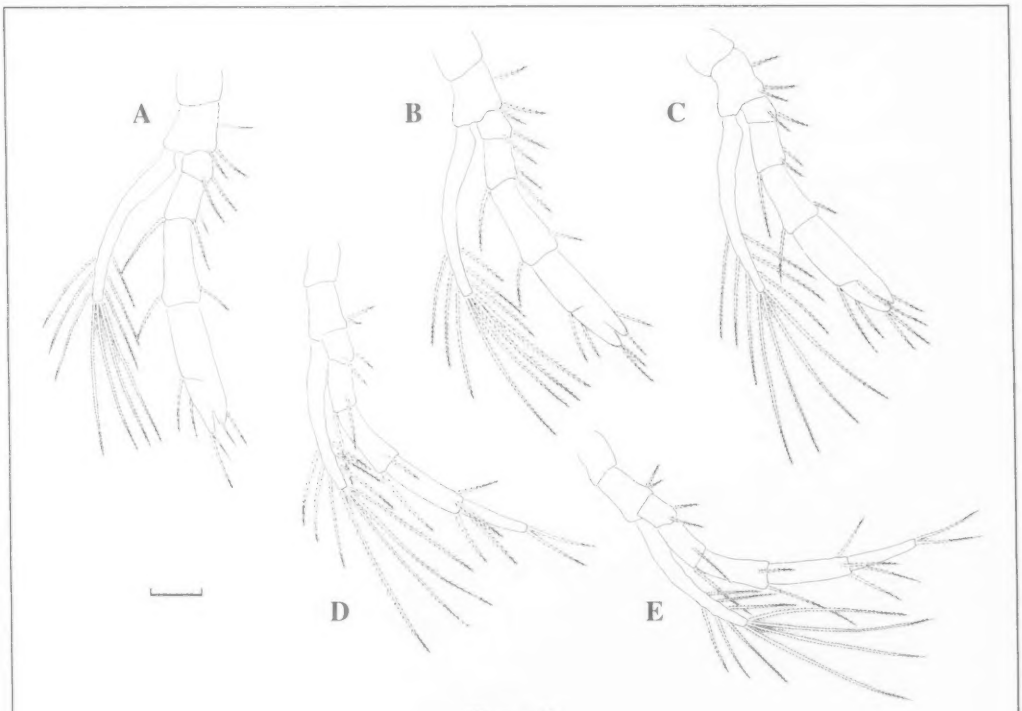

Figure 10

Metapenaeopsis dalei. Third mysis stage: (**A**) first pereiopod; (**B**) second pereiopod; (**C**) third pereiopod; (**D**) fourth pereiopod; (**E**) fifth pereiopod. Scale bar = 0.2 mm.

Body contour (Figs. 6G, 11I): Adult-like; pleopod developed; thorax completely covered by carapace; last five thoracic sternal plates with 2, 2, 0, 1, 1 spines.

Carapace (Fig. 6, G and H): Long rostrum with one epigastric tooth and three dorsal teeth; one pair of supraorbital, antennal, pterygostomial and hepatic spines anteroventral and posteroventral spines absent.

Antennule (Fig. 11A): Peduncle three-segmented, 1st segment with one large ventral spine, one small proximal spine, 40 plumose setae and a statocyst, 2nd segment with 10 plumose setae, 3rd segment with seven plumose setae; outer ramus two-segmented with 2, 6 aesthetascs; inner ramus two-segmented with 1, 3 plumose setae.

Antenna (Fig. 11B): Protopod unsegmented with two spines and one seta; endopod 23-segmented, 1st segment with two spines; scaphocerite with 34 marginal plumose setae, four spines on outer margin and 21 setae on surface.

Mandible (Fig. 11C): Denticulate setae absent; mandibular palp three-segmented, distal segment ovate; left mandible with 1, 10, 20 plumose setae; right mandible with 2, 11, 21 plumose setae.

Maxillule (Fig. 11D): Protopod two-lobed, coxal endite with nine plumose setae, basial endite with 22 naked setae; endopod four-segmented with 2, 2, 2, 3 setae.

Maxilla (Fig. 11E): Protopod four-lobed, endites with 11, 4, 10, 8 setae; endopod two-segmented with 8, 3 setae; scaphognathite with 43 plumose setae.

First maxilliped (Fig. 11F): Protopod two-lobed, coxal endite with nine setae and wo spinules, basial endite with 36 setae; endopod four-segmented with 2, 0, 1, 5 setae; exopod with 10 plumose setae.

Second maxilliped (Fig. 11G): Naked podobranch, basis with 16 setae; endopod five-segmented with 8, 15, 1, 9, 10 setae; exopod with six plumose setae.

Third maxilliped (Fig. 11H): Coxa with three setae, basis with six setae; endopod five-segmented with 13, 12, 9, 13, 9 setae; exopod with eight plumose setae.

First pereiopod (Fig. 12A): Coxa with four setae, basis with four setae; endopod 5-segmented and fully chelate with numerous setae; exopod with 8 plumose setae.

Second pereiopod (Fig. 12B): Coxa with one seta, basis with two setae; endopod five-segmented and fully chelate with numerous setae; exopod with 8 plumose setae.

Third pereiopod (Fig. 12C): Coxa naked, basis with five setae; endopod five-segmented and fully chelate with numerous setae; exopod with 10 plumose setae.

Fourth pereiopod (Fig. 12D): Coxa naked, basis with four setae; endopod five-segmented with numerous fine setae; exopod with 11–12 plumose setae.

Fifth pereiopod (Fig. 12E): Similar to 4th pereiopod in form; exopod with 7–8 plumose setae.

First pleopod (Fig. 12F): Uniramous; two-segmented, proximal segment with 3–5 setae, distal segment with 10–14 plumose setae.

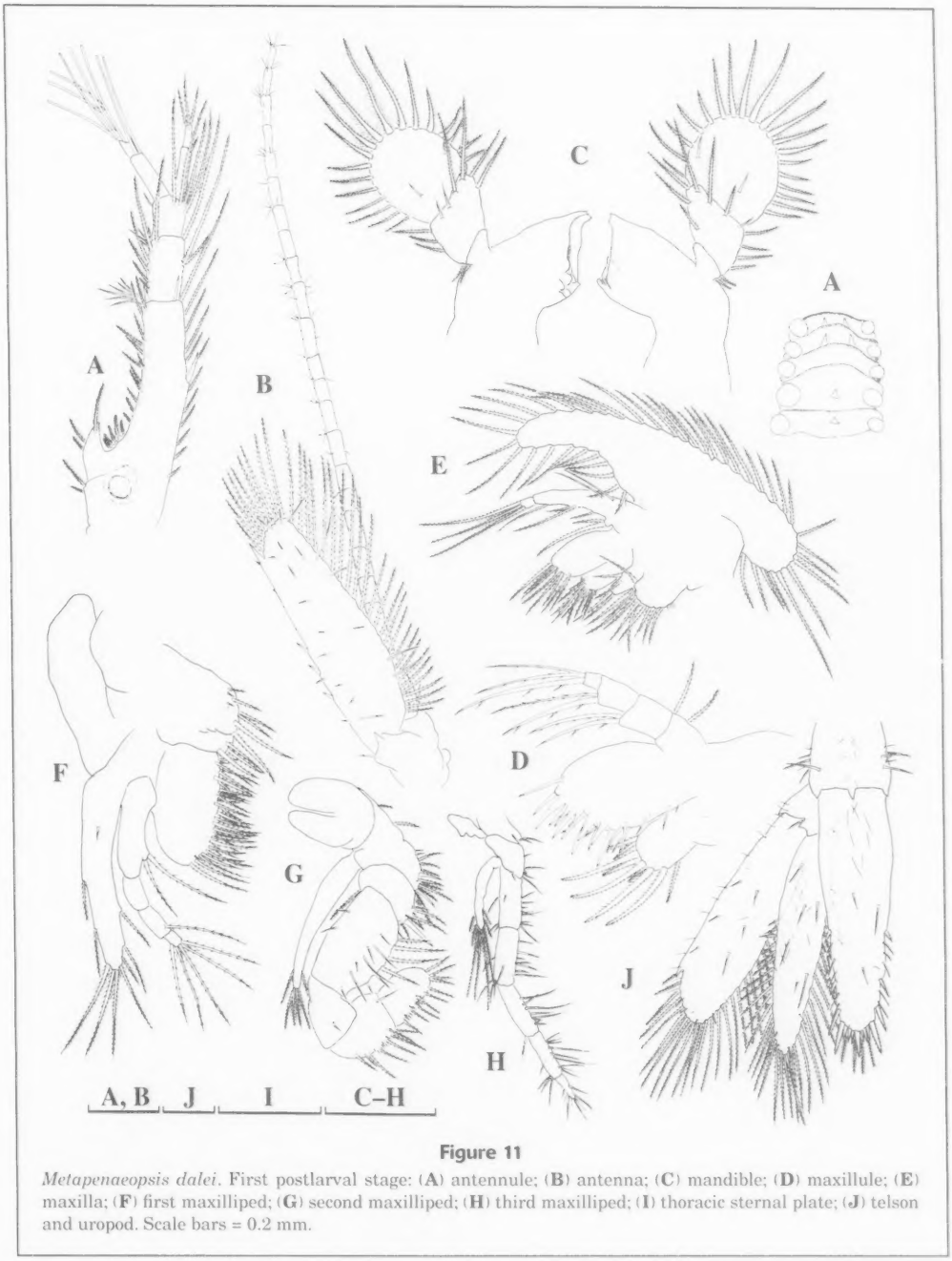

Figure 11

Metapenaeopsis dalei. First postlarval stage: (**A**) antennule; (**B**) antenna; (**C**) mandible; (**D**) maxillule; (**E**) maxilla; (**F**) first maxilliped; (**G**) second maxilliped; (**H**) third maxilliped; (**I**) thoracic sternal plate; (**J**) telson and uropod. Scale bars = 0.2 mm.

Second pleopod (Fig. 12G): Similar to 1st pleopod.

Third pleopod (Fig. 12H): Similar to 1st pleopod, with 19 setae.

Fourth pleopod (Fig. 12I): Similar to 1st pleopod, with 18 setae.

Fifth pleopod (Fig. 12J): Similar to 1st pleopod, with 19 setae.

Abdomen (Fig. 6, G and H): One lateral spine on 5th and 6th abdominal somites, one dorsomedian spine and one pair of lateroventral spines on 6th abdominal somite.

Uropod (Fig. 11J): Protopod with two spines; endopod with 23 plumose setae; exopod one fused spine and 21 plumose setae; numerous fine setae on dorsal and ventral surface of both rami.

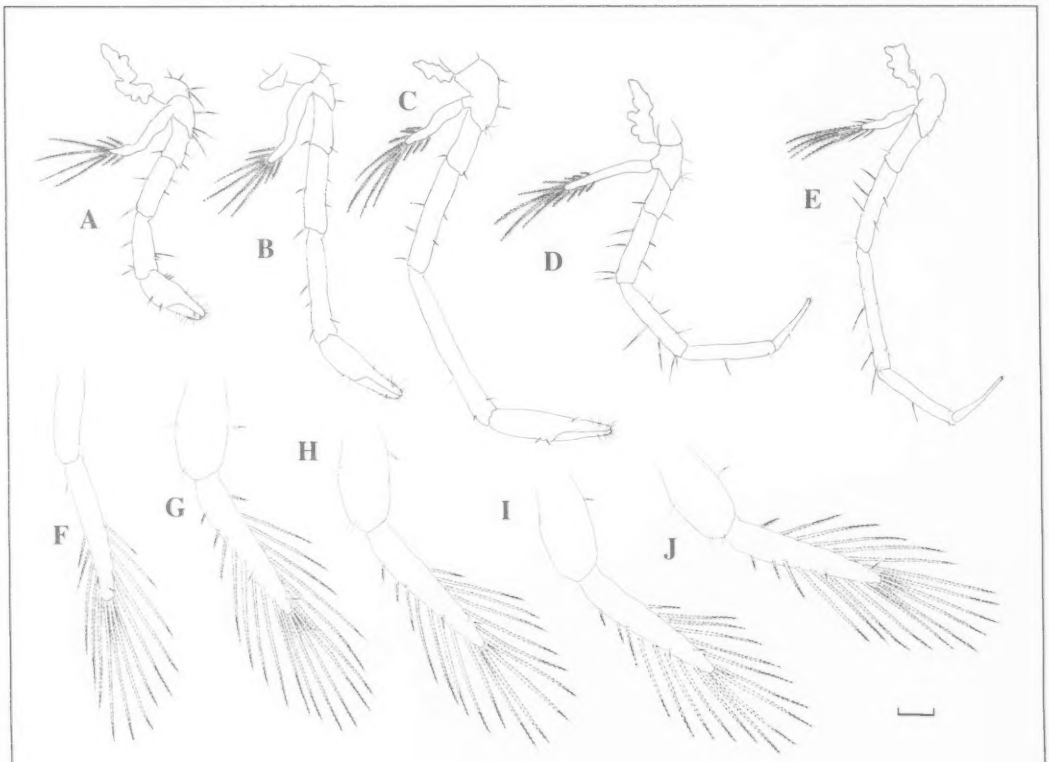

Figure 12

Metapenaeopsis dalei. First postlarval stage: (**A**) first pereiopod; (**B**) second pereiopod; (**C**) third pereiopod; (**D**) fourth pereiopod; (**E**) fifth pereiopod; (**F**) first pleopod; (**G**) second pleopod; (**H**) third pleopod; (**I**) fourth pleopod; (**J**) fifth pleopod. Scale bar = 0.2 mm.

Telson (Fig. 11J): Pointed, with seven pairs of setae, one posteromedian spine, and numerous fine setae on surface.

Discussion

Jackson et al. (1989) and Dall et al. (1990) used laboratory-reared and field-caught larvae, respectively, for their keys to the larvae and postlarvae of the penaeid genera. The protozoeal stages of the genus *Metapenaeopsis* can be distinguished easily from those of other genera by the 2nd antennal formula, mobile eyes, presence of strong spines above the frontal organ, and the body length. The mysis and postlarval stages are easily seperated from those of other genera by the serrated anteroventral margins of the carapace and unique thoracic sternal plate spines (2, 2, 0, 0, 0).

The first naupliar stage of *M. dalei* bears a chitinous conical protuberance on the posterodorsal aspect of the body. The cephalic knobs described for *M. stridulans* and *M. barbata* are also present from 3rd naupliar to 6th nauplius stages (Chong and Sasekumar, 1994; Ronquillo and Saisho, 1997). The protozoeal stages of *M. mogiensis, M. andamanensis, M. palmensis, M. stridulans, M. barbata,* and *M. dalei* have similar orbital or supraorbital spines, a telson setal formula of 7+7 and antennal setation of 0, 1; 5, 5 or 0, 1; 4, 5. However, five dorsomedian abdominal spines are found on the abdomen of the 3rd protozoeal stage of *M. dalei*, but three in *M stridulans* and *M. barbata*. The mysis and postlarval stages of *M. palmensis, M. stridulans, M. barbata,* and *M. dalei* are similar in general appearance, but some differences are found in the posterior ventral serrations of the carapace, in the number of setae on the scaphognathite and scaphocerite, and the thoracic sternal plate spines. Comparative morphological characteristics of *M. palmensis, M. stridulans, M. barbata,* and *M. dalei* are listed in Table 3.

The important morphological characters of the first postlarva of *M. dalei* that distinguish it from the rest are

1 43 scaphognathite setae on maxilla;
2 three scaphocerite spines on outer margin of antenna; and
3 sternal plate spines: 2, 2, 0, 1, 1.

Table 3

Comparison of larval morphological characteristics of *Metapenaeopsis palmensis*, *M. stridulans*, *M. barbata*, and *M. dalei*.

Developmental stage	Characters	*M. palmensis* (Jackson et al., 1989)	*M. stridulans* (Chong and Sasekumar, 1994)	*M. barbata* (Ronquillo and Saisho, 1997)	*M. dalei* (the present study)
Egg	diameter (mm)	—	0.697–0.729	0.220–0.570	0.325–0.375
Nauplius	shape	—	pandulate	oval	oval
Third stage protozoea	dorsomedian abdominal spines	5	3	3	5
First stage mysis	posterior ventral serrations on the carapace	absent	absent	absent	present
Third stage mysis	statocyst	present	absent	present	present
First stage postlarva	scaphognathite setae in maxilla	20	21	30–31	43
	scaphocerite spines on outer margine of antenna	1	2	2, 2, 0, 0, 0	3
	thoracic sternal plate spines	2, 2, 0, 0, 0	—	2, 2, 0, 1, 1	2

Acknowledgments

We are grateful to D. I. Williamson (Port Erin Marine Biological Station, Isle of Man, U.K.) and C. Sankarankutty (Universidade Federal do Rio Grande do Norte, Natal, Brazil) for critical reading of the manuscript. We thank H. K. Cha for collecting the gravid females of *Metapenaeopsis dalei*. We express our gratitude to the head of Taean Fish Hatchery, NFRDI, for providing us with experimental facilities. The authors wish to acknowledge the financial support of the Korea Research Foundation made in program year of (1998).

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Interannual variation in predation on first-year *Sebastes* spp. by three northern California predators

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Abstract–There is much interannual variation in numbers of first-year *Sebastes* that settle near shore off northern California, and when more abundant, they become prey of an increased variety of predators. Among predators that concentrate on these abundances are the black rockfish (*Sebastes melanops*); the blue rockfish (*Sebastes mystinus*); and the kelp greenling (*Hexagrammos decagrammus*). One might expect *S. melanops* to be involved in these attacks because it is known to be piscivorous, but *S. mystinus* and *H. decagrammus* ordinarily feed on invertebrates. The predation on *Sebastes* juveniles is concentrated during a relatively brief period shortly after they have settled in nearshore habitats. Most of this predation occurs during June and decreases sharply through July and August, and relatively little after that. We argue that the pattern of predation reflects removal of less adapted individuals during the period shortly after settlement.

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First-year *Sebastes* spp. off California vary greatly in number from year to year (Stephens et al., 1984; Love, et al., 1991), as do young-of-the-year of many marine fishes (Hjort, 1926; Cushing, 1973; Ricker, 1954). It has been argued that this variability between years is set during the earliest stages of life history, so that numbers present at settlement can be used to predict ultimate strength (or weakness) of year classes (Bailey and Spring, 1992; Myers and Cadigan, 1993; Ralston and Howard, 1995). But such predictions may need to consider postsettlement mortality, which has been recognized as a density-dependent force that reduces the interannual variation in year-class size evident at settlement (e.g. Sissenwine, 1984).

Early evidence that young-of-the-year (YOY) suffer density-dependent mortality after settlement came from studies of fishes caught by trawlers in temperate seas. Some of these studies identified predation as the main cause of this mortality (e.g. Lockwood, 1980), but most recognized predation as just one of several possibilities (Veer, 1986; Myers and Cadigan, 1993). More recently, investigators using scuba to observe underwater have studied postsettlement juvenile mortality in a variety of tropical and temperate species. Although some have concluded that this mortality is not density dependent (e.g. Victor, 1986; Sale and Ferrell, 1988), others have concluded not only that it is density dependent but also that it acts to regulate populations (Sano, 1997) and is a result of predation (Hixon and Carr, 1997; Steele, 1997). That predation is the major cause of mortality during and after settlement now seems generally accepted, and attempts are being made to identify the mechanisms involved under controlled conditions in laboratories (e.g. Bertram and Leggett, 1994; Witting and Able, 1995).

Although there have been many studies of the relations between predation and recruitment, all have been of short duration and thus limited as examinations of interannual variations. An opportunity to draw on 11 years of data for such a study developed from our work with marine communities off northern California. There, an investigation of trophic relations in fishes overlapped annual assessments of YOY *Sebastes* spp., and during this period (1977 to 1987) certain preda-

tors attacked the recently settled *Sebastes* only during years when these were more numerous.

Among predators drawn to YOY abundances were three of the region's most prominent species: the black rockfish (*Sebastes melanops*), the blue rockfish (*Sebastes mystinus*), and the kelp greenling (*Hexagrammos decagrammus*) (Fig. 1). The attacks by *S. melanops* might have been expected because this predator is known to prey regularly on a variety of fishes (Moulton, 1977; Rosenthal et al., 1988), but *S. mystinus* ordinarily feeds mainly on pelagic invertebrates (Gotshall et al., 1965; Hobson and Chess, 1988), and *H. decagrammus*, a benthivore with more varied food habits, feeds mainly on crustacea (particularly crabs), polychaetes, and mollusks (Moulton, 1977; Simenstead et al[1]).

Our objective was to determine when these varied predators attack YOY *Sebastes* spp., how this predation relates to changes in YOY abundance, and to identify implications for management.

Materials and methods

All of our studies on California's north coast involved using scuba to investigate organisms in their natural settings. Under these circumstances, we routinely noted events like settlement of juvenile *Sebastes* even when our attention was directed elsewhere. This feature of our work was important in enabling us to integrate elements of disparate studies in preparing this report.

Study area

The area of study was in 5–15 m of water within 300 m of shore, about 2 km north and south of Albion, in Mendocino County (lat. 39°13′N; long. 123°14′W). Because this coast is fully exposed to north Pacific seas, strong surge and turbulence prevailed most of the time. The ocean floor there consists mainly of irregular rock pavement and boulders (some 5–15 m in diameter) and isolated patches of sand.

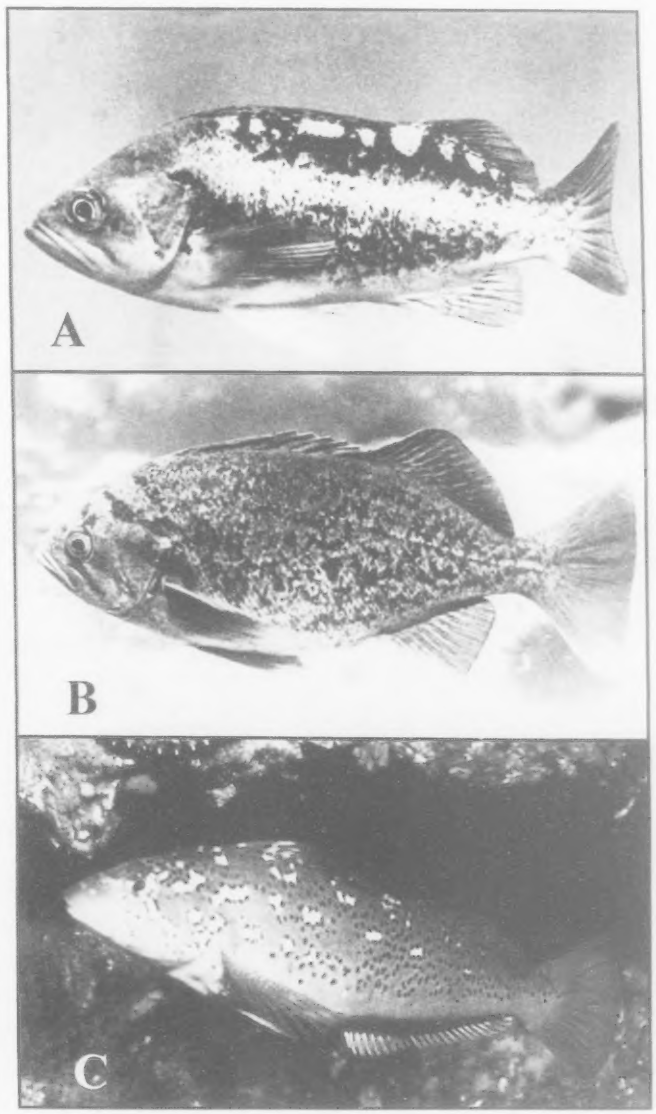

Figure 1

(**A**) Black rockfish, *Sebastes melanops*. (**B**) Blue rockfish, *Sebastes mystinus*. (**C**) Kelp greenling, *Hexagrammos decagrammus*. The black rockfish, with a larger mouth and a body form more conducive to speed, is morphologically better adapted than the other two species for running down and capturing elusive prey above the sea bed. The more oval shape of the blue rockfish suggests less need for speed in capturing its regular prey, whereas its smaller mouth and shorter snout (which increases an ability to simultaneously train both eyes on small targets close ahead) are more typical of planktivores than piscivores. Both rockfishes have a lower jaw that extends beyond the upper, which is consistent with attacking prey that are above the seabed, whereas the kelp greenling has an upper jaw that extends beyond the lower, for attacking prey that are on the seabed. Also, the kelp greenling's elongate body functions better swimming among, rather than above, the rocks.

[1] Simenstead, C. A., B. S. Miller, C. F. Nyblade, K. Thornburg, and L. J. Bledsoe. 1980. Food web relationships of northern Puget Sound and Straight of Juan De Fuca. Report to Marine Ecosystem Analysis (MESA), Puget Sound Project. U.S. Environmental Protection Agency, Washington, D.C. 20460, 335 p.

There are substantial seasonal changes in the habitat, particularly those associated with variable coastal upwelling (Bakun, 1973; Hobson and Chess, 1988). From late spring through fall, beds of bull kelp, *Nereocystis leutkeana*, form canopies at the sea's surface in many places, but most are swept away by storm seas during the subsequent winter. We began our study there in 1975, and the area, along with its flora and fauna, had become familiar to us by the time data presented in this report had been collected.

Measures of juvenile abundance

We had noted interannual variation in numbers of first-year *Sebastes* spp. as an incidental adjunct to more than 15 years of study in California's nearshore habitats, but were prompted to begin annual assessments of their abundance only after exceptionally large numbers settled along the north coast during 1977. At the outset, time available for this work was limited by other projects; therefore through 1982 our effort was directed mainly at developing means for identifying species. Features now used to distinguish *Sebastes* juveniles were at that time largely unknown, and of the three dominant forms settling in Mendocino habitats, only *S. mystinus* could be recognized at the outset. The other two juveniles—*S. flavidus* and *S. melanops*—remained indistinguishable until diagnostic features were determined by Laroche and Richardson (1980).

Despite the uncertain identities involved, one of us (ESH) estimated the relative abundance of YOY *Sebastes* present each year from 1978 to 1982 as a percentage of large total abundance in 1977. These estimates were made during the course of other projects and without consideration of publication, but nevertheless were recorded in field notes. Each annual estimate during these years represented a consensus based on repeated assessments (about weekly) between June and October, and although they lacked precision, they represented the only measures of YOY abundance for years that produced much of the data on predation. Some readers will dismiss these estimates as overly subjective, but others will appreciate the opportunity of considering all available evidence.

The annual assessments of YOY abundance became a major activity in 1983. By then, virtually all YOY *Sebastes* spp. seen underwater at the study sites could be identified, and we had developed standard procedures to assess their abundance. From that year on, YOY were counted during midday (1000 to 1400 h) at four sites within the study area. We attempted to make counts at least once each week but found that our ability to do so was determined largely by weather conditions The first counts each year were made shortly after the initial settlement of YOY, which occurred some time during late spring or early summer. The counts then continued through October, when it became evident that YOY of one major species—*S. flavidus*—were leaving the area.

During each assessment one to three of us swam at constant speeds close to the seabed, making frequent changes in direction. We counted the YOY *Sebastes* within 3 m of varied tract lines that traversed all major habitats represented at the sites. Because the highly variable turbidity and turbulence characteristic of this area strongly influenced our ability to see the fish, counts were made only when horizontal visibility exceeded 4 m and turbulence was not excessive. This limitation precluded a fixed schedule because counts were aborted more often than completed.

Assessments were made at widespread sites along the coast of northern California, from Mendocino southward to Marin; however, only data from Mendocino were used in this report because that is where the predators were sampled. Similarly, although juveniles counted in the environment were identified to species, our report refers to all as *Sebastes* spp. because they were compared with juveniles recovered from gut contents, which too often were damaged beyond recognition as species.

The study of trophic relations in *S. mystinus* included YOY, and although food habits of these lack relevance here, sizes of individuals sampled from June through October provide a measure of sizes available to predators during the first five months after settlement. This information has broad implications, because growth in *S. mystinus* is similar to growth in the vast majority of *Sebastes* YOY that settle in this habitat (except *S. paucispinnus*, which was not included).

Food habits of predators

The predators were sampled with scuba and hand-held spears throughout the 11 years of overlap between the two investigations. Only specimens with identifiable gut contents were used in this report. They were collected during midday (1000 and 1400 h), and all months were represented (Fig. 2). Specimens representing each species ranged upward in size from the smallest found with a YOY *Sebastes* among its gut contents. This eliminated from consideration the many specimens that were too small to include YOY among their prey. Each specimen was observed in its natural setting before capture, and many were collected as part of comprehensive assessments of the biota. Both of these circumstances contributed to interpretations of the gut contents.

Following capture, specimens were measured (standard length), and their digestive tracts were removed and preserved in 10% formalin. During later examination in the laboratory, the gut contents were removed and studied under magnification. Food items were identified to species when feasible, and the record of each prey taxon included number, size, stage of digestion, and percent contributed to the total diet. Much of this information is of limited interest here, but the last variable listed (labeled "percentage of diet" in the figures) was used to show the relative importance of each prey category as food. This measure was obtained by grouping elements of the various prey categories as they lay spread out in a petri dish, and then visually estimating the percentage that each category represented of the entire sample. Generally, values presented are means calculated from individual diets in specified groups of predators.

Juveniles of the highly distinctive *Sebastes jordani* were exceptions to the generalization that YOY *Sebastes* recov-

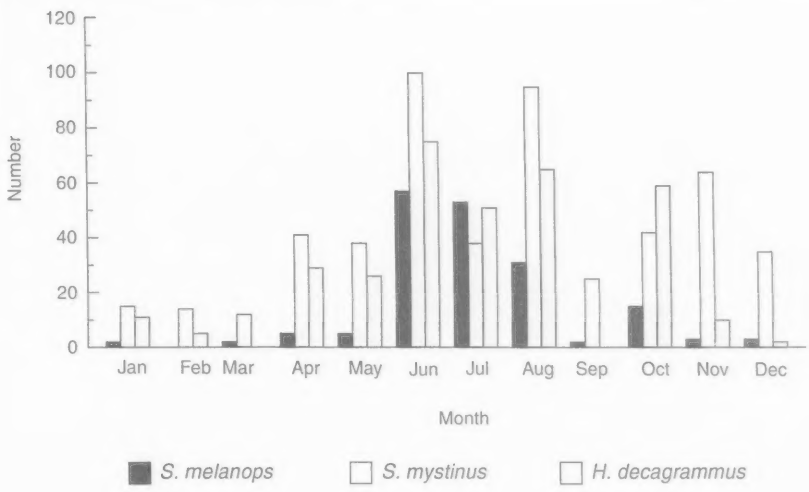

Figure 2

Monthly sampling of predators used in study of predation on YOY *Sebastes* spp. near shore off Mendocino.

ered from gut contents often had been damaged beyond recognition as species. Owing to their distinctive morphology, *S. jordani* juveniles were identifiable even when extensively damaged, but they are excluded from our report because they were in the study area for reasons other than those accounting for the presence of the other *Sebastes* species (Hobson and Howard, 1989).

Results

YOY *Sebastes*

The number of YOY *Sebastes* varied greatly from year to year (Fig. 3). Their initial appearance near shore tended to be earlier in the season during years of greater abundance; thus the earliest first sighting was during April of the year that YOY were most numerous (1987), and the latest first sighting was during June of the year that YOY were least numerous (1983). Upon arrival, these fish were <4.0 cm SL, often numerous, and still showed the silvery hues characteristic of their pelagic stage. Our record of first arrivals was limited. Ordinarily, visits to the Mendocino study sites at this time of year were separated by at least a week, sometimes up to a month (during extended periods of inclement weather), and our efforts were concentrated close to the seabed. Observations in the surface canopy of bull kelp came mostly during brief surveys following more extensive observations at greater depths. Once alerted to their presence, however, we intensified our search (even during the same day) and often found a few individuals or small groups among the rocks below. Most of these were 4.0 to 4.5 cm SL and showed darker hues more appropriate to reef settings.

Numbers of juveniles increased rapidly over the weeks that followed (except during years of low abundance, e.g. 1983) to reach maximum levels between mid June and early July. Throughout this time, and over subsequent months, the juveniles aggregated at varying distances from the seabed or kelp—some in mixed species aggregations. Their distance from these structures was influenced by the water's transparency, however, and this affected our ability to measure abundance. When visibility was reduced, as during phytoplankton blooms of late spring and early summer, the juveniles stayed closer to shelter—many often out of sight among the rocks. It was often difficult to assess their abundance under these conditions, even when visibility was sufficient to perform the counts. In contrast, when visibility was extended, as when oceanic waters flowed shoreward with relaxation of upwelling during the fall, the juveniles ranged farther from shelter and were readily counted. Thus, although the greatest numbers were recorded during a period of exceptionally clear water during July 1987, counts were at times higher during September or October than during June or July (Table 1), even though we assumed that there were fewer individuals present. This circumstance did not affect interannual comparisons because the pattern was basically the same each year, but it effectively precluded comparisons between months or seasons.

Sizes of YOY available to predators during the five months after settlement can be approximated from data of the YOY *S. mystinus* sampled from June through October for study of gut contents. The 82 from June were 3.7 to 5.8

Table 1

Number of YOY *Sebastes* counted during months after settlement (*n*=number of 1-min counts).

Year	May			June			July			August			September			October		
	date	*n*	no./min.	date	*n*	no./min.	date	*n*	no./min.	date	*n*	no./min.	date	*n*	no./min.	date	*n*	no./min.
1983		—			—		7 Jul	150	1.1		—		6 Sept	85	3.8		—	
1984		—		5 Jun	50	1.3		—		8 Aug	214	5.8		—			—	
										23 Aug	100	15.9						
1985	31 May	25	89.5	19 Jun	52	424.6	9 Jul	59	304.2	30 Aug	50	192.6		—			—	
							23 Jul	18	74.8									
1986		—		4 Jun	59	8.2	8 Jul	51	3.8	7 Aug	49	32.6	29 Sep	29	46.4	23 Oct	29	30.4
				24 Jun	37	47.9				26 Aug	53	16.4						
1987		—		30 Jun	32	81.2	14 Jul	42	220.9	12 Aug	32	210.8	1 Sep	51	606.7	19 Oct	10	133.2
							21 Jul	10	93.9	20 Aug	15	118.9	22 Oct	10	235.0			
							22 Jul	18	517.6									

cm, $\bar{x}$=5.2 cm SL; the 42 from July were 4.5 to 6.3 cm, $\bar{x}$= 5.4 cm SL; the 73 from August were 4.9 to 6.7 cm, $\bar{x}$= 5.6 cm SL; the 28 from September were 4.6 to 7.1 cm, $\bar{x}$= 6.2 cm SL; and the 46 from October were 5.8 to 8.0 cm, $\bar{x}$= 7.0 cm SL. Inferences based on these data can be extended to YOY of most *Sebastes* spp. in this setting because they grow at rates similar to *S. mystinus*. Another source for sizes of YOY *Sebastes* came from predator gut contents. There, individuals as small as 4.0 cm SL continued to be present throughout the three months of intensive predation, whereas individuals smaller than this were present only through June (Table 2).

It was evident that the YOY *Sebastes* remained where they had settled for at least five months. Over 90% of those counted at all sites from Mendocino to Marin were either *Sebastes mystinus* or *S. flavidus*. (The third species alluded to above, *S. melanops*, dominated shoreward of the census area and followed the same pattern of annual abundance.) Fidelity to specific locations was noted through the end of October, when representatives of *S. flavidus* left the area, presumably for deeper water.

Although this chronicle of YOY occurrence ends each year with counts made through October, during some years assessments continued through the winter and following spring. Results of these extended counts confirmed findings of others that juveniles of these species remain where they settle for at least a year (Love et al., 1991). That YOY *S. flavidus* left our study area for deeper water about five months after settlement may be related to Mendocino being toward the southern limit of its distribution. To the north, in Puget Sound (Moulton, 1977) and southeastern Alaska (Carlson and Barr, 1977), schools of juvenile *S. flavidus* have been observed at the same shallow sites for one to several years.

Predators and general features of predation

When diets of the predators during all months of all years are combined, the results (Fig. 4) generally are consistent with diets attributed to them in previous reports (e.g. Gotshall, et al., 1965; Rosenthal et al., 1988; Simenstad et al.[1]), except that *S. melanops* appeared even more piscivorous than the other *Sebastes* species. The extent that *S. melanops* was found to consume fishes, however, can be attributed to 79% of the specimens examined having been collected from June through August (compared with 45% of *S. mystinus* and 57% of *H. decagrammus*). In fact, all three species consumed more fishes during the summer than during other seasons, and most of the increase came from eating YOY *Sebastes* (Fig. 5). It is significant that all but 6 of 537 YOY *Sebastes* recovered from gut contents of the three predator species came from specimens collected during these three months. Most were consumed during June, and sharply decreasing numbers were taken through July and August (Table 3).

Interannual variation in predation on YOY *Sebastes*

There was much interannual variation in predation on YOY *Sebastes*, and it can be related to interannual varia-

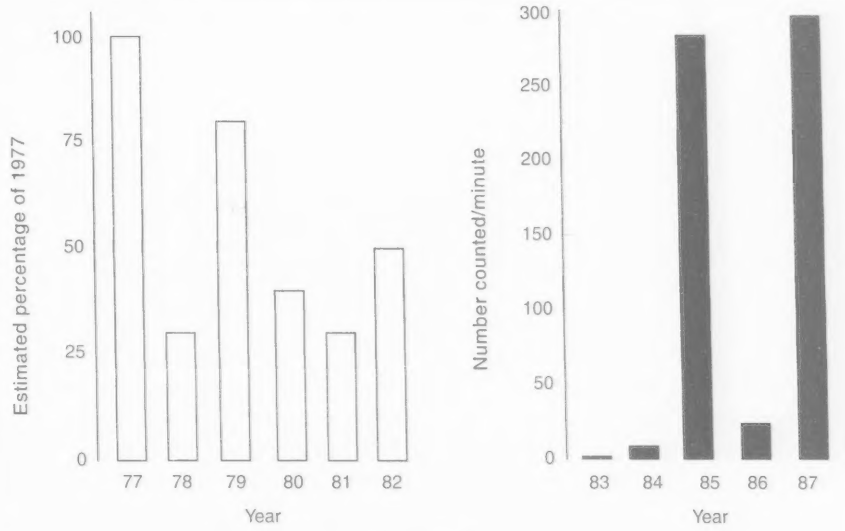

Figure 3

Annual measures of YOY *Sebastes* spp. near shore off Mendocino, 1977 to 1987. Measures representing 1977 to 1982 represent estimated proportions of the abundance observed during 1977. Measures representing 1983 to 1987 represent visual counts in the environment. The two panels, estimates and counts, are equated in the same way that the estimates of 1978–82 are related to those of 1977, i.e. by extracting from the 1985 field notes a consensus that abundance that year was approximately that of 1977. Each annual measure is the average of all individual samples from that year.

Table 2

Standard length (SL, in cm) of YOY *Sebastes* spp. recovered from gut contents (n=number for which size was recorded[1]).

	June		July		August	
Sebastes species	n	SL range	n	SL range	n	SL range
S. melanops	93	3.0–5.5	29	4.0–6.4	24[2]	4.0–8.0
S. mystinus	18	3.5–5.5	4	4.0–5.4	0	0–0
H. decagrammus	45	2.9–5.5	11	4.0–5.5	3	4.4–5.0

[1] Not all YOY recovered from gut-contents were measured. When samples included >2 individuals of one species, or indistinguishable as species, only the largest and smallest were measured. These samples were analyzed to characterize food habits and the intent of the analysis was simply to determine range of sizes consumed. Also, records of *S. paucispinus* are excluded because this species grows much faster than the others, and several individuals of the subject species were excluded because it was evident they were in their second year.

[2] Two distinct groups are included here (t=9.129, 4 df, P<0.001). Nineteen ranged from 4.0 to 6.0 cm SL, whereas the other five ranged from 7.0 to 8.0 cm SL.

Table 3

Number of YOY *Sebastes* spp. consumed by each of the three predator species during June, July, August, and during all other months, 1977–87 (values in parentheses=number predators examined that had gut contents).

Sebastes species	June	July	August	All other
S. melanops	313 (57)	44 (53)	40 (31)	1 (37)
S. mystinus	32 (100)	5 (37)	0 (95)	1 (286)
H. decagrammus	81 (75)	12 (51)	4 (65)	4 (142)

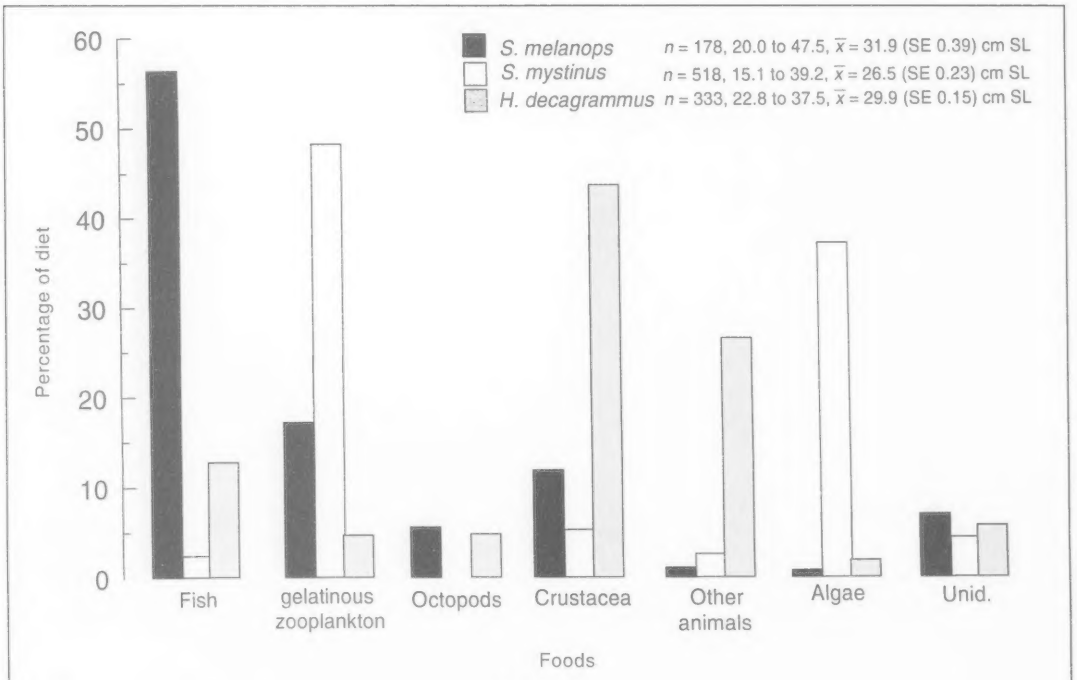

Figure 4

Foods consumed by the three predator species (*Sebastes melanops*, *S. mystinus*, and *S. decagrammus*) 1977–87 (*n*= individuals with identifiable food in gut).

tion in YOY abundance (Fig. 6). Evidence of predation was strongest during years when YOY were most numerous in the habitat (1977, 1979, 1985, and 1987), and there was virtually no evidence of predation during the years when YOY were least numerous in the habitat (1983, 1984, and 1986). Furthermore, it was only during the years that YOY were more numerous that we found them among the prey of *S. mystinus*—1985 being the year we found the most.

We saw no indication that distributions of adult *S. melanops*, *S. mystinus*, or *H. decagrammus* were influenced by the presence of YOY *Sebastes*. Even when YOY were most numerous, attackers seemed limited to residents of the immediate area. This finding should have been expected because each year's relative abundance was in effect coast wide.

Discussion

Much predation is opportunistic; thus predators often are drawn to concentrations of organisms that would not otherwise be their prey. Consider, for example, that when the squid *Loligo opalescens* deposits great masses of eggs on sediment off central California, various fishes, marine mammals, and birds converge from surrounding habitats to forage on what is for them an unusual food (Morejohn et al., 1978). Similarly, when the herring *Clupea pallasi* deposits eggs in great abundance on the seabed in San Francisco Bay, these become food for the brown rockfish, *Sebastes auriculatus*, which otherwise feeds mainly on decapod crustacea and fishes (Ryan, 1986). Another example is an incident during 1962 in the Gulf of California, where a 1-m moray eel (Muraenidae) was observed thrashing at the water's surface in a vigorous attempt to feed from a dense swarm of larval fishes, each no more than 1 cm long (Hobson, 1968). Certainly this predator was behaving in a manner that was contrary to its usual mode of feeding. So perhaps it should have been expected that YOY *Sebastes* in exceptionally large numbers would draw attacks from predators not otherwise prone to show them interest.

But the level of predation on YOY *Sebastes* off Mendocino involved more than relative abundance of prey. The attacks were concentrated during June, declined sharply through July and August, then remained at low levels during the rest of the year. This pattern did not follow the number of YOY present. These YOY gained abundance through most of June to attain maximum numbers late that month or during July, and then remained abundant after predation had subsided to low levels at the end of August. Often our counts of YOY were higher during September or October than during June or July, and although to a considerable extent this higher court was related to increased visibility in clear water, it nevertheless argues

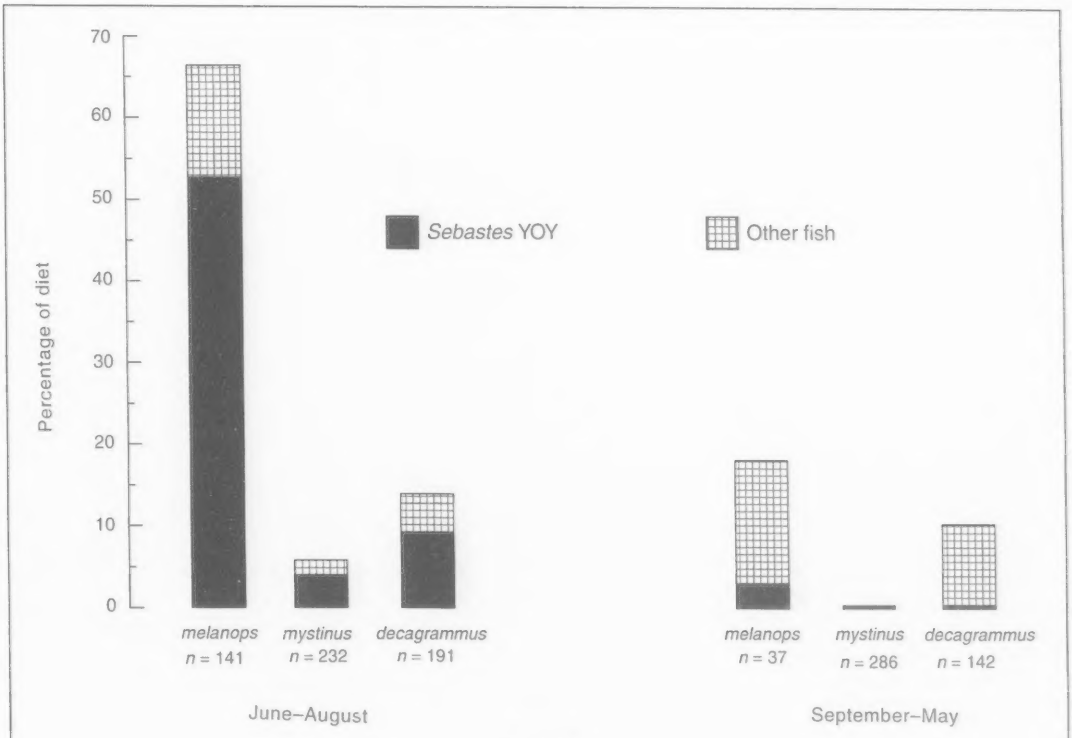

Figure 5

Fish in diet of the three predators (*Sebastes melanops*, *S. mystinus*, and *S. decagrammus*) June through August compared with September through May. YOY *Sebastes* spp. are distinguished from other fish. *n*=individuals with identifiable food in gut.

against attributing the precipitous decline in predation through late August simply to shortages of prey.

It has been widely reported that mortality among YOY of a variety of fishes is greatest during and immediately after settlement (e.g. Doherty and Sale, 1985; Victor, 1986; Shulman and Ogden, 1987), but there has been virtually no attempt to explain this finding, other than to implicate predation. We propose that the intense predation of early summer, and its subsequent sharp decline, mirrored a pattern of vulnerability among the YOY. Abilities critical for survival are quickness in responding to attacks, speed in attaining shelter, and the ability to use shelter that is available. And increasingly important with time is the ability to acclimate to novel situations—the capacity to learn. These abilities are based on inherent characteristics that can be expected to vary widely among individuals, with the more deficient being more vulnerable to predators. It follows that individuals most deficient are likely to be among those consumed during or shortly after settlement, whereas individuals progressively less deficient would be consumed in diminishing numbers over the following months.

Certainly other factors contributed to the decline in predation during the summer. That YOY decreased in number and increased in size must have influenced the intensity of predation. There is evidence that by summer's end most YOY had grown too large for predation by *S. mystinus* and *H. decagrammus*. The largest YOY *Sebastes* among the gut contents of either species were 5.5 cm SL (Table 2), and by September most in the environment were larger than this (based on growth evident in the representative *S. mystinus* sampled for study of food habits).

Other considerations, however, argue against the importance of prey-size in shaping the observed pattern of predation. *Sebastes melanops*, which is morphologically better suited than either *S. mystinus* or *H. decagrammus* to prey on fishes (Fig. 1), was able to feed on YOY *Sebastes* of up to at least 8.0 cm SL (Table 2), yet ate very few of them after August. Also, the great variation in size among predators, as well as in growth among YOY would be expected to dampen the effects of prey-size on population-level feeding intensity. Another consideration is the continued presence of YOY as small as 4.0 cm SL (Table 2) during the late-summer switch to other prey.

Although probably a combination of factors contributed to the decline in predation during the summer, we continue to consider that the concentrated attacks immediately after settlement are mostly likely elicited by the presence of inherently less-adaptive individuals. This is classic nat-

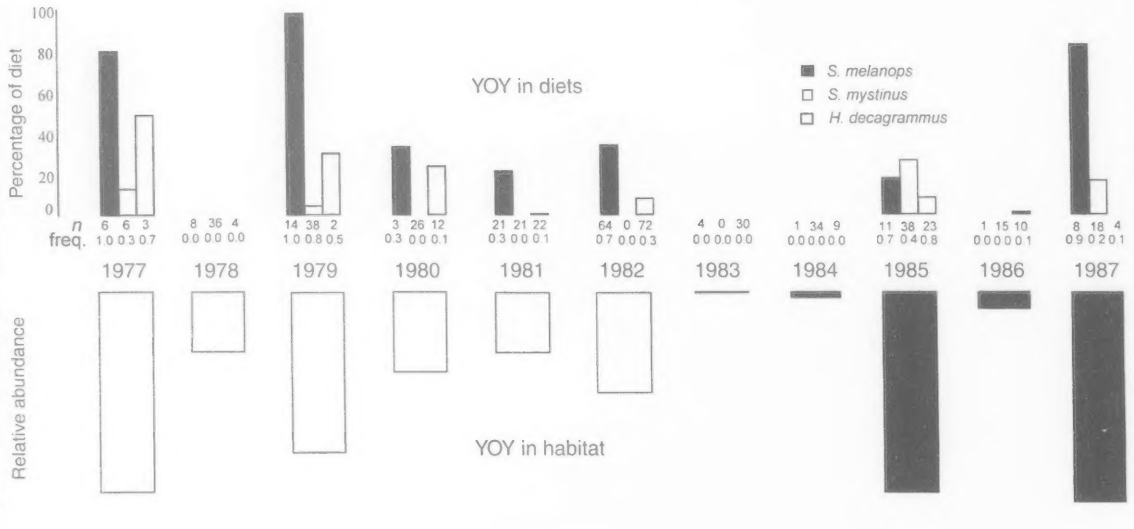

Figure 6

Inter-annual variation in occurrence of YOY *Sebastes* spp. in predator diets in relation to abundance of YOY in the habitats, June through August. Measures of YOY abundance in habitat are based on information presented in Figure 3. *n* = Individuals examined that had identifiable food in gut.

ural selection. That predators studied in our study had essentially resumed their regular diets by the end of summer indicated to us that YOY vulnerable to their attacks had by that time become scarce.

There are other predators that follow similar temporal patterns in feeding on YOY *Sebastes* off northern California. Pacific hake, *Merluccius productus*, for example, have been reported attacking YOY *S. jordani* so close to shore that many are driven onto the beach—but only during June and early July of years when these prey were particularly abundant (Hobson and Howard, 1989). Similarly, king salmon, *Oncorhynchus tshawytscha*, regularly switch to YOY *Sebastes* from other prey during late May and June, then switch back before the end of July (Adams et al.[2]). Other examples include *Sebastes* spp. studied by Hallacher and Roberts (1985) in kelp forests off Carmel, CA. In a chronicle that followed activities of these fishes over one year (with limited data from July and August of two other years), it was determined that *S. atrovirens, S. carnatus, S. chrysomelas,* and *S. melanops* fed primarily on YOY *Sebastes* during the "upwelling season" (April to August), but all except *S. carnatus* switched to invertebrates during the "non-upwelling season" (September to March). Hallacher and Roberts attributed this pattern to seasonal differences in YOY abundance.

The decline in attacks during the summer does not lead to essentially an end to predation on YOY, however. At least one resident piscivore, the ling cod, *Ophiodon elongatus*, remains a regular threat (Miller and Geibel, 1973). In fact, Adams and Howard (1996), studying in part the same series of assessments used in our study, considered predation the major cause of natural mortality in YOY *S. mystinus* from late summer through early spring. Their estimates were higher during years that YOY were more abundant, indicating persistent density-dependent predation, but were much lower than most other published rates of natural mortality for juvenile fishes, probably because they missed the intense predation of late spring and early summer. And although Hallacher and Roberts (1985) reported that most *Sebastes* spp. off Carmel switched to predation on invertebrates from September to March, they noted that *S. carnatus* continued to prey on YOY *Sebastes* during that period.

There is evidence that density-related predation continues to dampen interannual variation in year-class size through entry into the fishery, which for most *Sebastes* spp. is at about age 3–4 years (Ralston and Howard, 1995). Arguments for the importance of postsettlement mortality in establishing ultimate year-class size have emphasized the extended effect of this mortality (e.g. Sissenwine, 1984) but do not recognize the extent that mortality from predation is concentrated during a relatively brief period immediately after settlement. We suggest that management needs would be most effectively met by measuring year-class size soon after this period of intense predation.

[2] Adams, P. B., W. M. Samiere, and C. J. Ryan. 1986. Unpubl. manuscript. Prey selection and diet of marine chinook salmon, *Oncorhynchus tshawytscha*, 17 p. Natl. Mar. Fish. Ser., NOAA, Tiburon CA 94920.

Although a measure based on recruits entering the fishery would more accurately define the resource, there have been no effective methods developed to determine abundance at that point. And even if available, the lateness of such a measure would limit its effectiveness. An assessment made at the end of the first summer based on direct visual counts by underwater observers, as described above, is an effective compromise. The YOY are readily counted, much of the postsettlement mortality is included, and there is time to use the results in planning management strategy.

Acknowledgments

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Behavioral reactions of northern bottlenose whales (*Hyperoodon ampullatus*) to biopsy darting and tag attachment procedures

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Abstract—The effects of invasive or intrusive research techniques need to be thoroughly documented in order to satisfy appropriate standards of animal care. How cetaceans react to either biopsy darting or tag attachment procedures has been studied for several species, and considerable interspecific variability in responses has been demonstrated; however, few studies have compared reactions to both techniques. In the family Ziphiidae (the beaked whales) nothing has been previously reported on responses to either technique. We examined and compared the reactions of northern bottlenose whales (*Hyperoodon ampullatus*) to biopsy darting and tagging. Reactions to both these procedures were generally low-level and short-lived; stronger responses were given to hits than to misses. There was no statistical difference in observed response to tag versus biopsy hits. The prior behavioral state of the whales appeared to influence the magnitude of reaction to both hits and misses and thus may be an important factor to consider in such impact assessment. Whales lying still at the surface showed stronger reactions than traveling or milling animals. Sea state appeared to affect whether there was a reaction to misses. Whales were more likely to respond to a miss in calm sea conditions. No avoidance of the research vessel was observed following a tag or biopsy attempt, and in most cases whales approached the research vessel again within several minutes.

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The nonlethal firing of projectiles at whales and dolphins is increasingly being used, both in order to obtain skin and blubber samples (e.g. Lambertsen, 1987) and to attach data-recording or transmitting devices (e.g. Mate and Harvey, 1983; Goodyear, 1993; Baird, 1998; Mate et al., 1998). Data collected with these techniques are important for management and conservation purposes but may come at some cost (usually a behavioral disturbance) to the individuals involved. This cost may vary for different species or populations (see e.g. Schneider et al., 1998), therefore the impacts should be assessed each time a study is conducted.

Reactions of various species of cetaceans to biopsy darting have generally been mild (e.g. International Whaling Commission, 1989; Whitehead et al., 1990; Brown et al., 1991; Weinrich et al., 1991, 1992; Barrett-Lennard et al., 1996; Weller et al., 1997). The most common response is a "startle" reaction, although the level of reaction varies slightly between species, and also between populations and individuals. In contrast, the reaction of cetaceans to tagging with suction-cup–attached tags has been found to vary dramatically. Although reactions of killer whales (*Orcinus orca*) and Dall's porpoises (*Phocoenoides dalli*) to the technique were minor (Baird, 1994; Hanson and Baird, 1998), those of bottlenose dolphins (*Tursiops* sp.) were strong and relatively long-lasting (Schneider et al., 1998).

The family Ziphiidae (the beaked whales) is the second largest family of cetaceans, yet no studies have reported their reactions to tagging or biopsy techniques. In this paper we compare the reactions of northern bottlenose whales (*Hyperoodon ampullatus*) to both techniques and investigate factors affecting the behavioral reactions observed. These results are particularly relevant to agencies that grant research permits (e.g. the National Marine Fisheries Service in the USA), which often require some discussion of the implications of research techniques in terms of animal care. Additionally, assessment of the magnitude and duration of any behavioral response caused by the process of attaching a tag is vital in ensuring that the attachment of the tag does not confound the behavioral data it records.

Materials and methods

Field research took place off eastern Canada, approximately 300 km east of Halifax, Nova Scotia, over a submarine canyon termed the "Gully" (approximate position: 44°N, 59°W) during June–August 1996–98. All tagging or biopsy attempts were made opportunis-

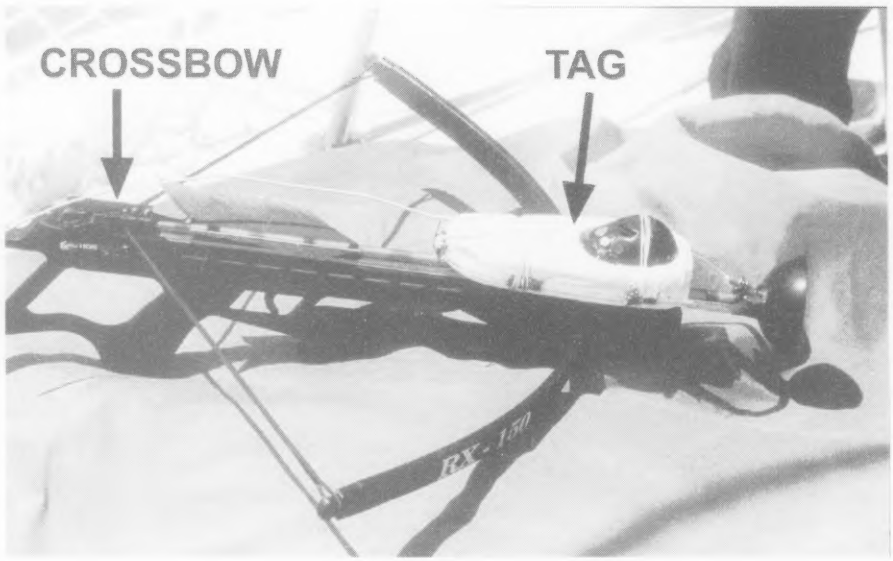

Figure 1

Photograph of the suction-cup–attached time-depth recorder and VHF radio tag ready to be deployed from a crossbow.

tically from a 12-m sailing vessel, operated under power at speeds of 1–4 knots.

The biopsy dart had a 2.5-cm-long, 0.6-cm-diameter cylindrical punch fitted with a dental broach (a barbed filament to hold a sample in place) (as illustrated in Barrett-Lennard et al., 1996), attached to the end of a standard crossbow bolt (total weight 28.5 g). A cylindrical stopper, set 2.5 cm back from the tip of the punch, caused the bolt to rebound after impact with the whale. Bolts were fired from a 67-kg-draw crossbow (Barnett WildCat XL) at a range of 5–15 m. Samples were usually taken from the flank near the dorsal fin. The floating dart was recovered and the skin and blubber sample was removed. The tissue was then subsampled for various analyses requiring either skin or blubber or both. The gender of the biopsied whales in this study was determined genetically (Gowans et al., 2000).

The tag measured 20 × 4 × 5 cm and had a 40-cm flexible antenna. The foam housing of the tag contained a time-depth recorder (Wildlife Computers, Redmond, WA, or AGO Environmental Electronics, Victoria, BC) and a VHF radio-transmitter (Advanced Telemetry Systems, Isanti, MN, or Telonics, Mesa, AZ). An 8-cm-diameter rubber suction cup (designed for automobile roof-racks, Canadian Tire) was used to attach the tag. The total unit weighed approximately 340 g in air. Tags were attached to a modified crossbow bolt (weight approximately 25 g) and were deployed with the same crossbow as described above (Fig. 1).

The group size and behavioral state of the whales prior to the biopsy darting or tagging attempt were noted. Group size was defined as the number of animals at the surface within five body lengths of each other (chain rule, see Smolker et al., 1992). Behavioral state was assigned as either logging (lying still or moving slowly in one direction at the surface) or milling or traveling (milling—moving slowly in no consistent direction; traveling—moving in a consistent direction at greater than 2 knots). Whenever possible, each tag or biopsy attempt was videotaped and this recording was used to confirm the consistency of behavioral categories assigned by different observers in the field for both before tagging attempt behavior and reaction. Attempts were classified as a hit or a miss; a hit was defined as contact with the whale and hits were further subdivided as to whether they were successful, i.e. whether biopsies obtained a sample or whether tags remained attached to the whale for more than 30 seconds. Sea state (Beaufort scale) was recorded every hour; sea state at the time of the biopsy or tag attempt was interpolated from these hourly logs. Categories of reaction types were defined following Weinrich et al. (1991):

1 No reaction: whale continued to show the same behavior as before the biopsy or tagging attempt;
2 Low-level reaction: whale modified its behavior slightly, e.g. dived rapidly or flinched;
3 Moderate reaction: whale modified its behavior in a more forceful manner but gave no prolonged evidence of behavioral disturbance, e.g. tail slap, acceleration, and rapid dive;
4 Strong reaction: whale modified its behavior in a succession of forceful activities, e.g. successive percussive behaviors (breaches, tail slaps).

Table 1

Number of whales showing different reaction-types to tagging and biopsy deployment attempts (percentages shown in parentheses).

Event	Reaction level: None	Low-level	Moderate	Total no. of whales
Tag-hit	2 (7%)	19 (65%)	8 (28%)	29
Biopsy-hit	3 (11%)	20 (74%)	4 (15%)	27
Tag-miss	33 (60%)	21 (38%)	1 (2%)	55
Biopsy-miss	16 (80%)	3 (15%)	1 (5%)	20

Goodness-of-fit G-tests were used to compare reactions to different techniques and under different conditions. Small sample sizes often necessitated pooling between categories. Because reactions to misses tended to be lower-level they were pooled between none and low to moderate, whereas reactions to hits tended to be higher-level and were pooled between none (or low) and moderate.

Results

Forty-seven biopsy attempts were made on northern bottlenose whales in 1996 and 1997 (Table 1). Of these, 27 attempts hit the whale and 20 obtained a skin and blubber sample. Six attempts hit, but did not retain a sample (primarily resulting from low hits at the water line). One dart sank after hitting a whale. Video footage was taken of 18 biopsy hits (15 successful) and 11 biopsy misses.

Eighty-four tagging attempts were made between 1996 and 1998 (Table 1). Twenty-nine attempts hit the whale but only six successfully attached (one for only 30 seconds). Video footage was taken of 15 tag hits (three successful attachments) and 34 tag misses.

The majority of whales showed no or low-level reactions to both tag and biopsy attempts (Table 1). No strong reactions were observed during our study. The whales reacted to 93% of the tag hits and 89% of the biopsy hits, but reacted to only 40% of the tag misses and 20% of the biopsy misses (Table 1). Reactions (categorized as none, low, or moderate) were significantly greater for hits than for misses (G=50.3, P<0.001, 2 df). Reactions to tag hits were not significantly different from the reactions to biopsy hits (G=1.51, P=0.47, 2 df). Of the 6 successful tag hits, 2 animals gave a hard tail flick, accelerated and dove (moderate reaction), 1 animal accelerated and dove, and 3 dove rapidly or flinched (low-level reactions).

The type of reaction to a hit was significantly related to the animal's behavioral state prior to the tagging or biopsy attempt (comparison for all hits of behavioral state (logging vs. milling or traveling) and reaction (none [or low] vs. moderate) G=4.04, P=0.044, 1 df). Low-level reactions were most common for traveling or milling whales, whereas logging whales were more likely to show stronger reactions, especially to tag hits (Fig. 2). There was also a similar relationship between behavior and reaction to misses, although whales rarely showed a moderate reaction to a miss (comparison of behavioral state [as above] and reaction [none vs. low or moderate] G=4.02, P=0.045, 1 df, Fig. 2). Reactions to hits of animals in groups were similar to those for lone individuals (G=0.767, P=0.38, 1 df). There was an effect of sea state on reaction type, but only for missed shots (comparison of sea state [≥Beaufort 2 with Beaufort <2], G=4.38, P=0.036 1 df, Fig. 3). This effect was greater for tag misses (G=6.80, P=0.009, 1 df) than for biopsy misses (G=2.41, P=0.12, 1 df).

Table 2

Gender of biopsied whales (n=20) and respective reactions.

Gender	Reaction level: None	Low-level	Moderate	Total no. of whales
Male	0	5	2	7
Female	2	9	2	13

No avoidance of the research vessel was observed after tagging or biopsy attempts. For the majority of attempts, animals remained at the surface. If the animals made a shallow dive, they usually returned to the research vessel within a few seconds or were photographed again within a few minutes of the tagging or biopsy attempt (for 82% of all attempts, whales returned to the surface and remained with the research vessel for at least five minutes). There was little difference in the likelihood of encounters ending within five minutes between tagging and biopsy attempts or between hits and misses. Furthermore, encounters including tagging or biopsy attempts were not shorter in duration than encounters without any tagging or biopsy attempt (one-tailed t-tests, P>0.05).

No significant difference between the reactions of males and females was found (G=2.1, P=0.35, 2 df, Table 2), but samples sizes were small and did not adequately represent the population.

Discussion

The response rate of northern bottlenose whales to biopsy hits (89%) was greater than that found for baleen whales (right whales, *Eubalaena glacialis*, 19%; Brown et al., 1991; humpback whales, *Megaptera novaeangliae*, 50%, Weinrich et al., 1991), but was similar to that recorded for other odontocetes. A 100% response rate was found for sperm whales (*Physeter macrocephalus*) (Whitehead et al., 1990) and for bottlenose dolphins (Weller et al., 1997), and an 81% response rate was found for killer whales (Barrett-Lennard et al., 1996). Reactions of bottlenose dolphins consisted of an observable short-term change in behavior (Weller et al., 1997). Momentary shakes or accelerations were observed for killer whales (Barrett-Lennard et al.,

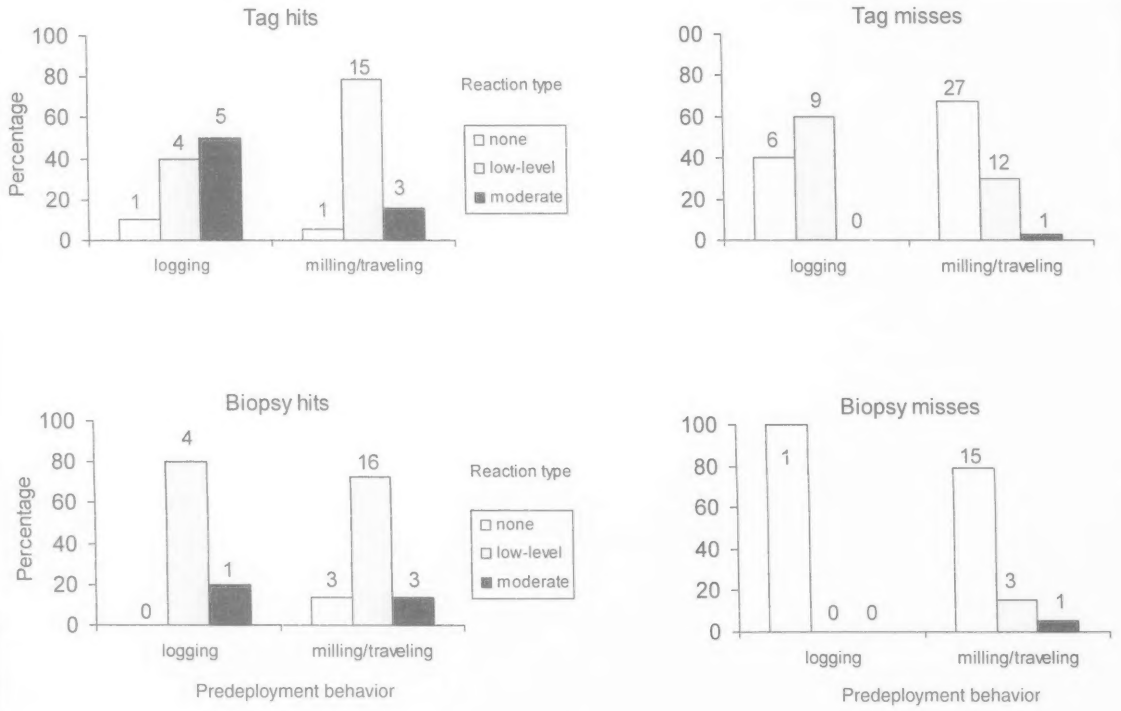

Figure 2

Relationship between behavioral state and reaction type for tag and biopsy deployments. Reactions during logging behavior were stronger than for other behaviors for both hits (P=0.044) and misses (P=0.045). Percentage of each reaction-type is displayed for each prebiopsy behavioral category (number of reactions of each type are shown above each bar).

1996), whereas sperm whales showed strong startle reactions, occasionally involving defecation (Whitehead et al., 1990). Reactions of bottlenose whales seemed most similar to killer whale reactions, i.e. relatively "low-level." Gender-related differences in the levels of reaction have previously been noted for humpback whales (Brown et al., 1994), although no such effects were found in this study.

Reactions of northern bottlenose whales to suction-cup tag deployment were also low-level. Bottlenose whales reacted to 93% of tag hits and 40% of tag misses. Baird (1994) documented only minor reactions by killer whales to crossbow-deployed suction-cup–attached tags: 52% reaction to hits and 26% reactions to misses. Reactions of short-finned pilot whales (*Globicephala macrorhynchus*) to the same tags deployed by crossbow consisted of a tail flick and rapid dive (Baird[1]). Similar variation in reaction has been observed from suction-cup–attached tags deployed by pole. Little reaction was observed to tags deployed on Dall's porpoise (Hanson and Baird, 1998) or pantropical spotted dolphins (*Stenella attenuata*; Baird[1]), whereas bottlenose dolphins showed prolonged and intense reactions to tagging attempts, reacting to 100% of hits and 71% of misses (Schneider et al., 1998). The scale of reaction for northern bottlenose whales appears to lie in the middle of this range.

As noted, reactions to tag hits were similar to reactions to biopsy hits, despite the fact that tags weigh substantially more than biopsy darts. A potential explanation for this is the variation in "tag hit" under our definition: some of the tag hits were glancing blows and so may have had little striking impact, whereas others were direct hits. In contrast, the impact of biopsy darting was more consistent (i.e. there were virtually no glancing hits for biopsy darts). In addition, the greater weight of the tags resulted in a slower delivery speed, thus the force of a heavier, slower-moving tag may have been similar to that of the lighter, faster-moving biopsy dart. Alternatively, animals may have a set reaction to any impact, such that the same response will be elicited unless some threshold is exceeded (perhaps through excessive or repeated impact).

As many authors have pointed out, evaluating short and long-term reaction to tag attachment is important in determining whether the presence of tags affects the recorded behavior (White and Garrott, 1990; Walker and Boveng, 1995; Croll et al., 1996). Data were recovered from two of

[1] Baird, R.W. 1999. Unpubl. data. Biology Department, Dalhousie University, Halifax, NS, B3H 4J1 Canada.

the six successful tag attachments and one of these tags was equipped to record velocity (Hooker and Baird, 1999). The whale's initial reaction to the attachment of the tag was a rapid acceleration and dive. The velocity record showed that this initial increase dropped within the first two minutes to levels observed for the rest of the deployment (Hooker and Baird, 1999). The general behavior of all six tagged whales (in terms of surfacing intervals and dive durations) was also consistent with that observed from nontagged whales. Thus, although based on a small sample size, it appears that the target animals' behavior is modified for only a few minutes in a short-term reaction to the tagging procedure.

Previous studies that examined responses to biopsy darting have been criticized because of the potentially confounding effect of the research vessel approach (Brown et al., 1994). In our study, the behaviors of the whales when first sighted did not change in any noticeable way during the approach of the research vessel for photo-identification, and immediately prior to the tagging or biopsy attempt. Thus we are relatively confident that the reactions we observed were due to the tagging or biopsy darting, rather than to the proximity of the research vessel. However, the approach of the research vessel may have caused subtle changes in behavior that we did not observe.

The major cue to which bottlenose whales react appears to be the physical impact of the tag or biopsy, because reaction to hits was much greater than reaction to misses (Table 1). Whales also appear to react to an acoustic or other sensory cue, evidenced by their stronger reactions to tag misses in calm sea conditions (when the hit would be more audible or the splash more likely to be detected above background levels; Fig. 3).

The primary factor affecting the reaction of bottlenose whales to either tag or biopsy stimulus appears to be the behavior of the whale at the time of the stimulus. The relative stimulus of a biopsy or tag is less for whales involved in traveling or milling than for whales lying still at the surface (Fig. 2). Similarly, differences in the level of reaction have been observed for humpback whales involved in different activities. Reactions of migrating humpback whales were generally lower than those of whales on feeding or breeding grounds (Brown et al., 1994), and mothers or primary escorts of humpback whales (thought to be involved in breeding activity) showed less reaction than other whales on the breeding grounds (Clapham and Mattila, 1993). Such results have wide implications for monitoring the effect of various activities (e.g. noise pollution) on cetaceans because the likelihood of reaction may vary depending on behavioral state.

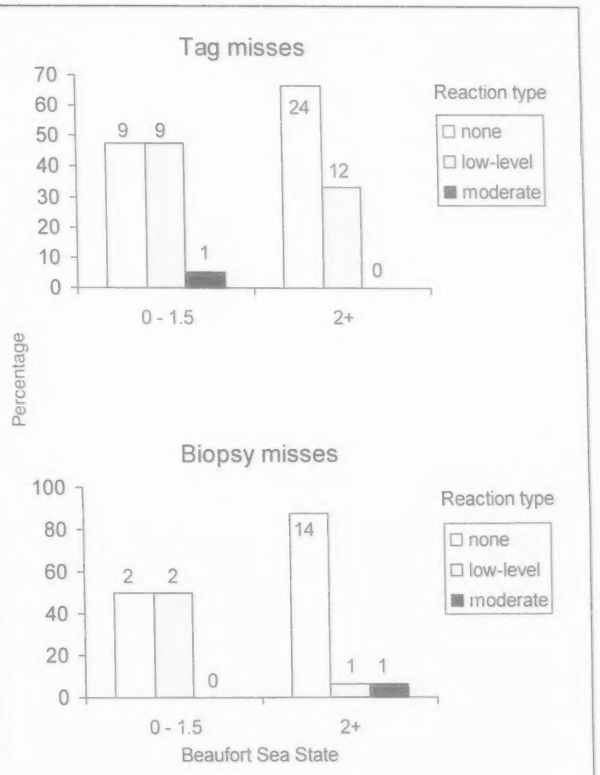

Figure 3

Relationship between sea state and reaction type for tag and biopsy misses. Reactions to misses were greater in calm (<Beaufort 2) than in rough (≥Beaufort 2) sea states (P=0.036). Percentage of each reaction-type is displayed for these two Beaufort sea state categories (number of reactions of each type are shown above each bar).

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Depth distributions and time-varying bottom trawl selectivities for Dover sole (*Microstomus pacificus*), sablefish (*Anoplopoma fimbria*), and thornyheads (*Sebastolobus alascanus* and *S. altivelis*) in a commercial fishery

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Abstract–We estimated size-specific depth distributions and commercial bottom trawl fishery selectivities for Dover sole (*Microstomus pacificus*), shortspine thornyhead (*Sebastolobus alascanus*), longspine thornyhead (*S. altivelis*), and sablefish (*Anoplopoma fimbria*) along the U.S. west coast. Depth distributions are size-specific because fish migrate ontogenetically to deep water. With ontogenetic migration, fishery selectivities of commercial bottom trawls depend on depth of fishing because large fish are most common in deep water. Depth distributions were similar for northern and southern areas and for males and females. Results show ontogenetic migration in sablefish, suggest a possible weak ontogenetic migration in longspine thornyhead, and confirm ontogenetic migration patterns already reported for Dover sole and shortspine thornyhead. Fishery selectivities varied among species, between areas, and changed dramatically over time for most species as fishing effort moved into deep water. Our approach used biological data collected during research bottom trawl surveys but was generally not affected by size selectivity of bottom trawl survey gear. Uncertainty in our commercial bottom trawl selectivity estimates was mostly from length-specific capture probabilities (or vulnerabilities) for fish in the path of commercial bottom trawls. Our estimates complement selectivity estimates from stock assessment models. The approach may be useful whenever the geographic distribution of fish depends on size or age, fishing effort is not randomly distributed geographically, and survey estimates of fish density, bathymetric data, and commercial fishing effort information are available.

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In our study, we estimated depth distributions and fishery selectivities for four demersal fish species taken in commercial bottom trawls: Dover sole (*Microstomus pacificus*), shortspine thornyhead (*Sebastolobus alascanus*), longspine thornyhead (*S. altivelis*), and sablefish (*Anoplopoma fimbria*). The fishes in our study were all valuable components of the deep-water commercial bottom trawl fishery off Washington, Oregon, and California (Pacific Fishery Management Council, 1998). Depth distributions for many fishes in the deep-water fishery depend on length and age because of ontogenetic migration (movement to deep water as fish grow and age, Jacobson and Hunter, 1993; Jacobson and Vetter, 1995). Depth distributions and ontogenetic migration are important because they affect many aspects of the deep-water fishery, including selectivity of commercial bottom trawls, which are the primary fishing gear.

Fishery selectivities measure the relative intensity of fishing mortality on fish of different size or age (Megrey, 1989). Fishery selectivities depend on size for fishes in the deep-water bottom trawl fishery (Perez-Comas, 1996) because of factors that include size and shape of mesh, size and shape of fish, orientation of netting, twine material (Wileman et al., 1996), and (as shown below) depth of fishing. In many length-structured stock assessment models, for example, the size-specific fishing mortality rate ($F_{y,L}$) in year y for fish in length class L is separated into the product of year-specific fishing mortality (F_y) and size-specific selectivity parameters (s_L), so that $F_{y,L} = F_y\, s_L$ (Megrey, 1989). Selectivities are typically scaled so that the selectivity for a reference size or age is one (Deriso et al., 1985; Methot, 1990). By convention, we scaled selectivities so that the length group with the highest fishing mortality rate had a selectivity of one.

Selectivities determine how fishing affects the size and age structure of a fish stock. They are used in stock assessment models to relate length and age composition data from catch samples to length and age composition of the stock. They are important in predicting effects of harvest rates (Legault, 1998) and in calculating biological reference points (e.g. $F_{0.1}$, F_{rep}, $F_{35\%}$, F_{max}, see Clark, 1991) used to recommend catch levels. At the policy and legal levels, they are often

involved in defining overfishing and rebuilding overfished stocks as required under U.S. law (Restrepo et al., 1998).

Estimating selectivity patterns for commercial fishing is a central issue in use of most stock assessment models based on forward simulation calculations (e.g. Deriso et al., 1985; Methot, 1990; Fournier and Archibald, 1982; Jacobson et al., 1994). Changes in fishery selectivity patterns over time may be difficult to measure if length or age composition data are not available for some years. When fishery length or age composition data are available, they can often be explained equally well by many different assumptions about fishery selectivity and population length or age composition. To understand this, consider the catch in number (C_L) of a single size group (length L) from a population. If the fishing mortality rate (F) is low and the selectivity for the size group is s_L, then $C_L = N_L F_y s_L$. Even if F_y is known, the resulting catch C_L could be from a high N_L and low s_L, low N_L and high s_L, or an infinite number of intermediate combinations. Problems are compounded if the operation of the commercial fishery and selectivity parameters have changed over time (Sampson, 1993; Brodziak et al., 1997; Rogers et al., 1997) or if natural mortality is also a function of size or age. For example, Tagart et al. (1997) found that scarcity of large female fish in fishery length-composition data was explained equally well by two models. One model had constant natural mortality and fishery selectivity decreased with size. The other model had constant fishery selectivity and natural mortality increased with size.

In our study, we estimated fishery selectivities for the commercial bottom trawl fishery using a new approach that complements estimates from stock assessment models. Our approach is based on information available in many fisheries, including data from bottom trawl surveys, information about bathymetry of fishing grounds, fishing effort data from logbooks, and length- or age-specific vulnerabilities to commercial fishing gear from field experiments. First, we used Jacobson and Hunter's (1993) method with our bottom trawl survey and bathymetric data to estimate depth distributions for fish of different lengths. Next, we used a new method based on commercial fishing logbook data, bathymetric information, length-specific vulnerabilities (from field experiments with commercial fishing gear) and depth distributions to estimate fishery selectivities in the commercial bottom trawl fishery. Our approach may be useful whenever the geographic distribution of fish depends on size or age, when fishing effort is not randomly distributed geographically, and when both survey densities and commercial fishing effort data are available.

Our results show clear differences in commercial fishery selectivities among species, areas, and over time. In addition, our analysis provides new information on depth distributions of sablefish and more precise understanding about depth distributions of Dover sole and shortspine and longspine thornyheads.

Materials and methods

All depths in this study are measured in fathoms (fm). Our study area was the continental shelf and upper continental slope at depths of 100–700 fm (equivalent to 183–1280 m) along the west coast of the U.S. between 36°00′ and 48°30′N (Fig. 1). We divided the study area near the Oregon–California border into southern (36°00′N to 43°00′N) and northern (43°00′N to 48°30′N) subareas to account for geographic differences in groundfish habitat, bottom trawl fishery and logbook data, and to accommodate areas defined for management of the groundfish fishery. The boundary 43°00′N separates the Eureka and Columbia INPFC (International North Pacific Fisheries Commission) management areas.

Areas (km^2) of each 100-fm stratum (estimated from spherical projections at sea level) were the same as those used by the National Marine Fisheries Service (NMFS) to estimate fish density and swept area abundance (Lauth[1]). The shallowest depth stratum in our study (100–199 fm) was relatively larger in the northern subarea (24%) than in the southern subarea (16%, Fig. 1; Tables 1 and 2). Fishing effort shifted into deep water earlier in the south (Tables 1 and 2). Fishing effort data from the southern subarea were collected mostly from California logbooks, whereas fishing effort data from the northern subarea were mostly collected from Oregon and Washington logbooks.

Survey data

Data from eight NMFS bottom trawl surveys on the upper continental slope in our study area were used to estimate depth distributions (Table 3). Each survey was conducted during October–December from the National Oceanic and Atmospheric Administration (NOAA) ship *Miller Freeman* (e.g. Lauth, 1997a, 1997b; Lauth, 1999). As a group, the surveys covered the entire study area (Fig. 1). A NMFS standard Nor'eastern otter trawl net with a 27.2-m headrope, 37.4-m groundgear, 89-mm codend mesh and a 32-mm mesh liner was used in each bottom trawl survey. In each survey, bottom trawl stations were allocated roughly in proportion to the area of 100-m depth strata (100–199, 200–299, 300–399, 400–499, 500–599, and 600–699 fm). Tows with poor gear performance, outside the study area, and at depths greater than 699 fm or less than 100 fm were excluded from our study. Lengths of Dover sole captured in surveys were recorded as total length (TL) in mm. Lengths of other species were recorded as fork length (FL) in mm.

Fishing effort data

Bottom trawl fishing effort data (hours towed) for the northern (Table 1) and southern area (Table 2) were obtained from logbooks submitted by commercial vessels operating out of ports in Washington (1985–97), Oregon (1978–97), and California (1978–96). The fishing effort data in our study were nominal (as reported) hours towed for bottom trawl tows in which the catch of Dover sole, thornyheads, or sablefish was greater than zero.

[1] Lauth, R. 1998. Personal commun. Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way, BIN C15700, Seattle, WA 98115-0070.

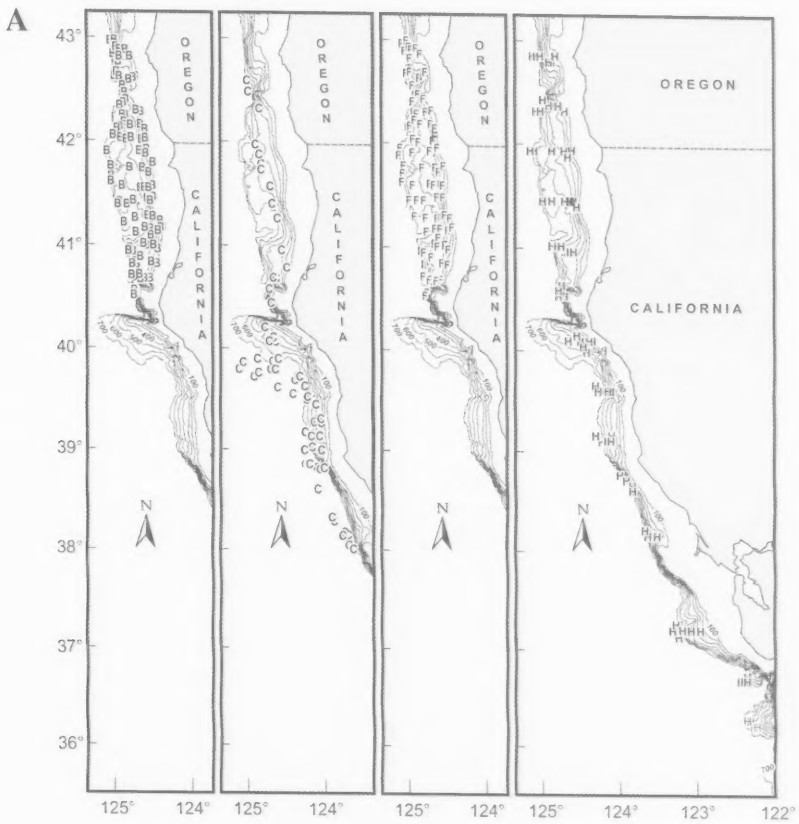


Figure 1

(**A–C**): study areas, 100–199, 200–299, 300–399, 400–499, 500–599, and 600–699 fm depth contours, and location of National Marine Fisheries Service bottom trawl survey tows used to estimate gear selectivities in the commercial bottom trawl fishery. Letters A–H are map symbols defined in Table 3 that identify locations of tows from different bottom trawl surveys.

Depth distributions

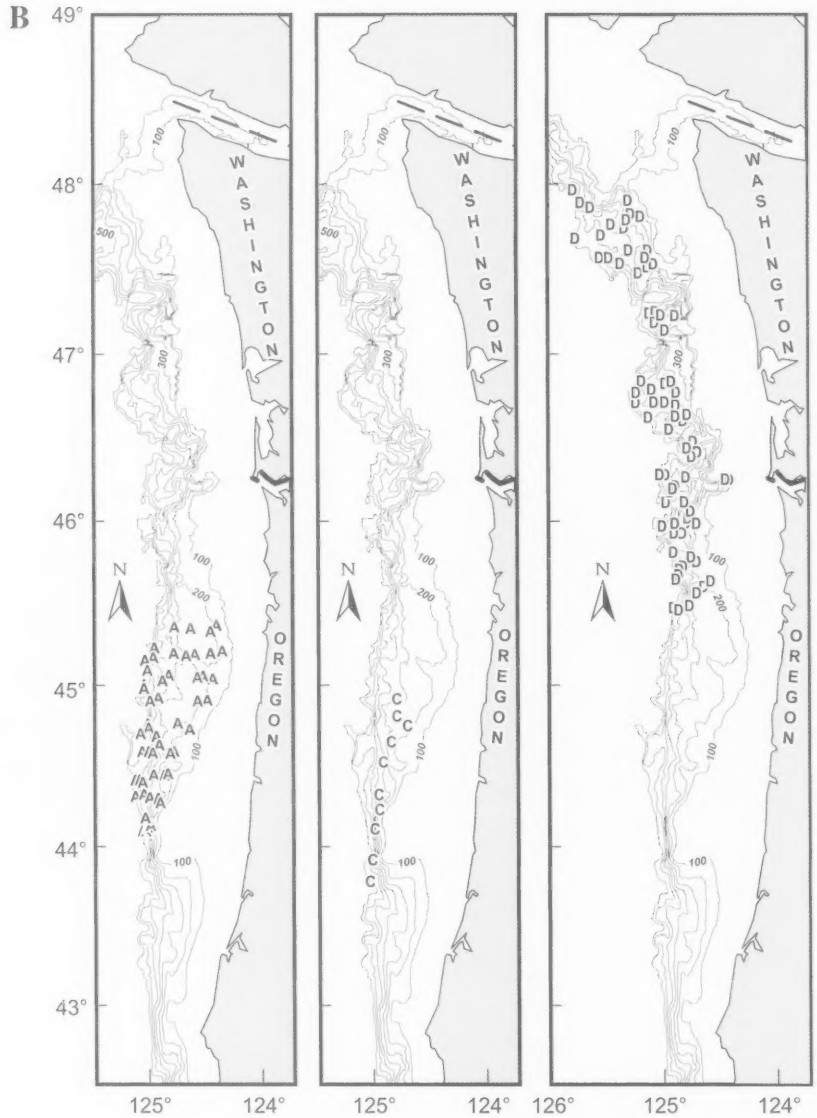
All calculations were based on fish length (two centimeter length groups), rather than fish age, because insufficient survey age data (see below) were available. The smallest and largest length groups in our analysis were "plus" groups. For example, a plus group of 20 cm at the low end of length composition would include fish 20 cm FL and smaller. We chose the largest and smallest length groups to use the widest possible range in lengths and to achieve reasonable precision and smoothness in commercial bottom trawl selectivity and depth distribution estimates for large and small fish.

For each species, depth distributions in the total population were estimated by conditional probabilities ${}^{s}p(d \mid L)$ which gave the odds, based on data from bottom trawl survey s, of finding a fish of length L at depth d in the population (Jacobson and Hunter, 1993). Following Jacobson and Hunter (1993), we used Bayes's theorem and data from a single bottom trawl survey in the estimator:

$$ {}^{s}p(d \mid L) = \frac{p_s(L,d)}{p_s(L)} = \frac{p_s(L \mid d)\, p_s(d)}{p_s(L)}, \qquad (1) $$

where the joint probability distribution $p_s(L,d)$ gives the probability that a randomly selected fish taken in bottom trawl survey s was length L and from depth stratum d. $P_s(L)$ is the probability that a randomly selected fish taken in the survey was length L. Other terms are defined below.

It is important to note that ${}^{s}p(d \mid L)$ refers to an estimate for the total population based on data from survey s (leading superscript notation), and terms on the right-hand side of the equation refer to the portion of the population selected by the gear used for survey s (trailing subscript notation). The total and surveyed populations differ because survey bottom trawls tend to select fish of certain size or ages and, depending on a variety of conditions, length composition data from survey catches will differ



from the length composition of the population (Gunderson, 1993). Our estimates of depth distributions for the total population $^{*}p(d \mid L)$ were generally unaffected by bottom trawl survey gear selectivity because selectivity of the survey gear affects both $P_s(L,d)$ and $P_s(L)$ equally and "cancels out." This important point is explained further below, after other terms in Equation 1 are defined.

For each bottom trawl survey, species, and depth stratum, length composition of the surveyed population $p_s(L \mid d)$ was calculated as a weighted average of length composition data from each tow in the stratum:

$$p_s(L \mid d) = \frac{\sum_t p_{s,t}(L \mid d) w_{s,d,t}}{\sum_t w_{s,d,t}}, \quad (2)$$

where $p_{s,t}(L \mid d)$ = the length distribution from tow t, and
$w_{s,d,t}$ = the tow catch rate (fish/m^2).

Tow catch rates were computed as $w_{s,d,t} = n_{s,d,t} / a_{s,d,t}$, where $n_{s,d,t}$ is the total number of fish caught and $a_{s,d,t}$ is the area swept (width of the net times distance towed).

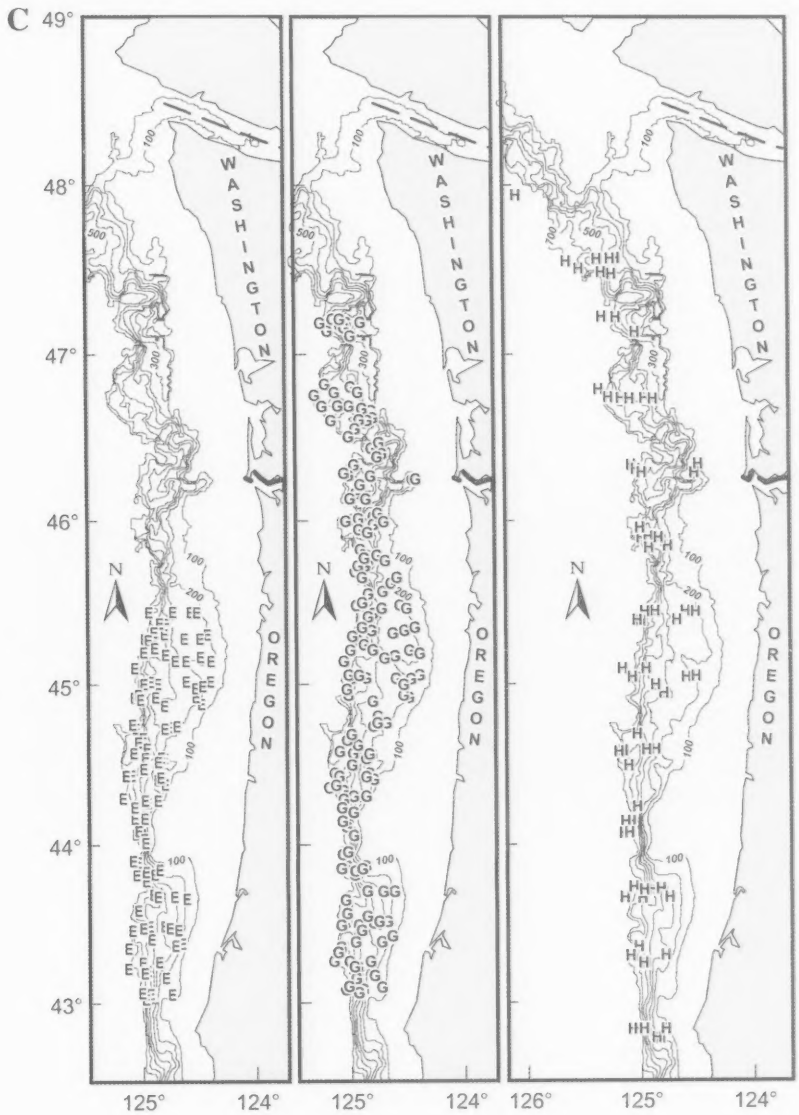


Figure 1 (continued)

The marginal distribution $p_s(d)$ gives the proportion of the surveyed population (all sizes and ages) in depth stratum d based on data from the bottom trawl survey:

$$p_s(d) = \frac{\overline{W}_{s,d} A_{s,d}}{\sum_d (\overline{W}_{s,d} A_{s,d})}, \quad (3)$$

where $\overline{W}_{s,d}$ = the average (weighted by area swept) catch rate in stratum d; and
$A_{s,d}$ = the total area (km^2) of the survey stratum.

The length distribution of the surveyed population $p_s(L)$ was calculated by summing the joint distribution for depth and length across depth strata:

$$p_s(L) = \sum_d p_s(L,d). \quad (4)$$

Data collected from the surveyed population on the right-hand side of Equation 1 can be used to estimate depth distributions for the total population because bot-

Table 1

Depth stratum area (in 1000 km²), percentage of total area, and nominal fishing effort (h/yr) by depth stratum for bottom trawls in the northern subarea (43°00′N–48°30′N) during 1978–96. Nominal fishing effort was calculated from Oregon and Washington bottom trawl logbook data as total hours trawled for trips catching any thornyheads, Dover sole, or sablefish.

		Depth (fm)					
		100–199	200–299	300–399	400–499	500–599	600–699
	Area	5.213	4.159	3.131	2.970	3.055	2.925
Year	% total area	24	19	15	14	14	14
1978		4224	1059	269	6	0	0
1979		4808	2991	1744	117	0	0
1980		1910	1277	811	46	5	0
1981		3669	1725	1215	118	0	0
1982		6955	5172	2252	263	16	0
1983		5942	4211	2089	354	23	0
1984		4845	4542	2026	235	0	0
1985		9086	6568	3017	1224	14	0
1986		6541	5680	1934	237	0	0
1987		9083	7639	2864	425	0	0
1988		12,762	12,874	5293	706	31	6
1989		15,125	17,458	7609	1792	1793	45
1990		13,820	14,070	8571	7020	4674	314
1991		19,346	20,148	13,346	7547	2976	221
1992		15,063	15,191	12,977	12,233	5467	595
1993		22,571	20,027	14,144	13,202	10,498	2262
1994		13,531	13,569	10,239	12,773	10,531	1634
1995		13,318	10,225	8502	11,117	15,580	2578
1996		13,539	10,867	8745	9831	12,831	1673

tom trawl survey gear selectivity cancels out. To prove this important point algebraically, note that

$$p_s(L,d) = \frac{{}^s\Pi(L,d)\sigma_{s,L}}{\sum_d \sum_L {}^s\Pi(L,d)\sigma_{s,L}} \quad (5)$$

and

$$p_s(L) = \frac{{}^s\Pi(L)\sigma_{s,L}}{\sum_d \sum_L {}^s\Pi(L,d)\sigma_{s,L}}, \quad (6)$$

where ${}^s\Pi(L,d)$ = the joint probability of depth and length in the total population when the bottom trawl survey was carried out;

${}^s\Pi(L)$ = the marginal probability distribution for length in the total population; and

$\sigma_{s,L}$ = the length specific selectivity for the survey bottom trawl gear (assumed the same in all depth strata, see "Discussion" section).

Use Equation 1, substitute terms from Equations 5 and 6, and simplify to get ${}^sp(d\,|\,L) = {}^s\Pi(L,d)/{}^s\Pi(L) = {}^s\Pi(d\,|\,L)$, where ${}^s\Pi(d\,|\,L)$ is for depth distributions in the total population. This proof shows that selectivities ($\sigma_{L,s}$) for bottom trawl survey gear cancel out, and that length-specific depth distributions ${}^sp(d\,|\,L)$ from Equation 1, based on bottom trawl survey data, are algebraically equivalent to length-specific depth distributions in the total population ${}^s\Pi(d\,|\,L)$. Of course, depth distributions are statistics that include uncertainty (measured by CVs in our analysis) due to survey data measurement errors and natural variability in survey selectivities (particularly natural variability that depends on depth).

Effects of survey gear selectivity on depth distribution estimates can be understood intuitively. Consider a hypothetical bottom trawl survey in our study area designed to measure abundance of a fish stock that consists of a single, 1-cm length group. As long as the selectivity of the survey bottom trawl was the same in each depth interval, the survey would measure the relative abundance of the length group in each depth stratum (N_d) and the relative abundance in the whole study area ${}^sN = \sum {}^sN$. The depth distribution for the hypothetical stock could be computed simply as ${}^sp(d\,|\,L) = N_d/N$ and the selectivity of the survey bottom trawl would not matter.

We averaged depth distributions estimated from different bottom trawl surveys ${}^sp(d\,|\,L)$ to use all available information. Preliminary results showed that survey-specific depth distributions were similar but relatively noisy. Aver-

Table 2

Depth stratum area (in 1000 km^2), percentage of total area, and nominal fishing effort (h/yr) by depth stratum for bottom trawls in the southern subarea (36°00′N –43°00′N) during 1978–96. Nominal fishing effort was calculated from California and Oregon bottom trawl logbook data as total hours trawled for trips catching any thornyheads, Dover sole, or sablefish.

		Depth (fm)					
		100–199	200–299	300–399	400–499	500–599	600–699
	Area	3.472	3.293	3.732	3.733	3.716	3.158
Year	% total area	16	16	18	18	18	14
1978		8584	4606	8673	3533	743	46
1979		11,707	6980	11,792	4035	1973	50
1980		8200	4992	6765	3171	817	95
1981		9346	7518	11,163	3635	1246	6
1982		10,941	7997	10,698	5142	1559	15
1983		19,481	13,375	17,037	9382	1662	62
1984		10,471	7972	8262	6090	2031	5
1985		13,642	8599	9603	7629	4782	41
1986		8914	10,861	11,228	8184	5262	60
1987		7496	8890	7712	5057	4001	191
1988		10,143	8839	5384	7575	9843	206
1989		8646	9120	6834	10,016	11,533	398
1990		7615	8630	6297	8459	12,717	345
1991		9408	15,428	11,660	8493	6776	567
1992		8327	14,616	12,602	10,356	10,873	512
1993		8424	13,488	15,861	9170	13,142	1241
1994		5999	9522	10,444	8452	13,743	3649
1995		8892	12,556	13,966	13,588	14,573	1542
1996		9825	13,766	15,608	13,549	9688	1887

Table 3

National Marine Fisheries Service (NMFS) bottom trawl slope survey data used to estimate depth distributions for Dover sole, shortspine thornyhead, longspine thornyhead, and sablefish. The National Oceanic and Atmospheric Administration ship *Miller Freeman* and standard bottom trawl survey gear (NMFS poly Nor'eastern otter trawl with small mesh liner, see text) were used in all surveys. Only tows with satisfactory performance were used. "Cruise ID" gives codes used in NMFS cruise reports. "Map symbols" are used in Figure 1.

Cruise ID	Start and end	Min and max latitude (°N lat.)	Min and max depth (fm)	Number of tows used	Map symbols
889	Nov 1988	44.11	121	53	A
	Dec 1988	45.37	682		
9011	Oct 1990	40.52	122	101	B
	Nov 1990	42.97	680		
9112	Oct 1991	38.39	108	83	C
	Nov 1991	45.34	684		
9210	Oct 1992	45.51	109	76	D
	Nov 1992	48.00	692		
9312	Oct 1993	43.07	101	110	E
	Nov 1993	45.50	683		
9512	Oct 1995	40.53	120	105	F
	Nov 1995	42.96	672		
9615	Oct 1996	43.09	102	199	G
	Nov 1996	48.07	690		
9711	Oct 1997	36.31	103	151	H
	Nov 1997	48.07	689		

aging depth distributions was reasonable because effects of survey bottom trawl selectivities (that may have differed because of area or year) were removed. Uncertainty in depth distributions was measured with coefficients of variation (CV) for average depth distributions from standard formulas for weighted means (see "Discussion" section for other approaches).

Fishery selectivities for commercial bottom trawls

The catch equation (C=F$\overline{N}$, Ricker, 1975) holds for each depth stratum. Consequently, total catch by the fishery is the sum of catches in all depth strata

$$C_{y,L} = \sum_{d} F_{y,d} V_L \overline{N}_{y,d,L}, \quad (7)$$

where $F_{y,d}$ = a year- and depth-specific instantaneous fishing mortality rate multiplier;
V_L = length-specific vulnerability to commercial bottom trawl gear (the probability that a fish in the path of the fishing gear is captured); and
$\overline{N}_{y,d,L}$ = average abundance during year y.

Vulnerabilities, like selectivities, were scaled to a maximum of one. Thus, the fishing mortality rate in a depth stratum for length groups fully vulnerable to the gear (V_L=1) is $F_{y,d}$ and the corresponding rate for other length groups is $F_{y,d}V_L$.

Depth-specific fishing mortality rates $F_{y,d}$ are related to nominal fishing effort at depth divided by the area of the depth stratum:

$$F_{y,d} = \frac{cE_{y,d}}{A_d}, \quad (8)$$

where $E_{y,d}$ = nominal effort (hours towed) for bottom trawls in depth stratum d during year y; and
c = a constant proportional to average area swept per unit time (Paloheimo and Dickie, 1964).

Depth-specific fishing mortality ($F_{y,d}$) is inversely proportional to stratum area (A_d) because the fraction of the stock harvested after an hour of fishing in a small area will be larger than the fraction harvested after an hour of fishing in a large area (Jacobson and Hunter, 1993).

Vulnerabilities (V_L) measure the probability of capture for a fish of length L given that the fish is in the path of the trawl. For this study, we calculated vulnerabilities using the logistic function based on length:

$$\eta_L = 2\log_e(3)\left(L - \frac{L_{50}}{R}\right), \quad (9)$$

so that

$$V_L = \frac{e^{\eta_L}}{1+e^{\eta_L}}, \quad (10)$$

and L_{50} = the length at which vulnerability is 50%. R is the difference between the predicted lengths at V_L=75% and V_L=25% for commercial bottom trawls with 4½-inch mesh codends (i.e. L_{75}–L_{25} in Perez-Comas, 1996). Four and one-half inch mesh is the current legal minimum in bottom trawls along the west coast. We rescaled values from Equation 10 so that the largest value was one.

Table 4

Parameter estimates from Perez-Comas (1996) and Perez-Comas[1] for logistic vulnerability models. All estimates are from alternate haul experiments and for commercial bottom trawls with 4½-inch diamond mesh codends fished from commercial trawlers in the west coast groundfish fishery off northern California, Oregon, and Washington (34°40′N–48°30′N and east of 126°W) during 1988–90. L_{50} is the length at which vulnerability is 50% and R is the difference between the predicted lengths at 75% and 25% vulnerability. SE is the estimated standard error for a statistic. Parameter estimates for shortspine thornyhead were also used for longspine thornyhead.

	L_{50} (cm)	SE (cm)	R (cm)	SE (cm)
Dover sole	33.8	1.01	3.96	1.22
Shortspine thornyhead	30.1	1.90	9.81	1.85
Sablefish	33.6	2.43	8.53	2.36

[1] Perez-Comas, J. A. 1998. Personal commun. Columbia Basin Research, School of Fisheries, Univ. Washington, Puget Sound Building, 1325 Fourth Ave., Seattle, WA 98101.

For Dover sole and shortspine thornyhead, we used species-specific vulnerability parameter estimates (Table 4) from Perez-Comas (1996). For sablefish, we used unpublished estimates (Perez-Comas[2]) estimated in the same manner. Perez-Comas's estimates were from paired bottom trawl experiments. The experiments measured vulnerability of fish of different sizes in commercial bottom trawls in relation to vulnerability in bottom trawls with 3-inch (between knots) mesh codends as a reference standard (see "Results" and "Discussion" sections for information about possible bias due to escapement of small fish from commercial bottom trawls with 3-inch mesh codends).

We assumed that vulnerability estimates for longspine thornyhead were the same as for shortspine thornyhead because no other information was available for longspine thornyhead. The two species are similar in shape and their size ranges overlap (shortspine thornyhead grow larger), but their depth distributions differ (Jacobson and Vetter, 1995).

Given vulnerabilities at length for commercial bottom trawls, an expression for commercial fishery selectivities at length can be derived because $p(d\,|\,L)\ N_{y,L} = N_{y,d,L}$, where $p(d\,|\,L)$ is for the total population computed as the average of $^{y}p(d\,|\,L)$ from each of the surveys. Substituting

[2] Perez-Comas, J. A. 1998. Personal commun. Columbia Basin Research, School of Fisheries, Univ. Washington, Puget Sound Plaza Building, 1325 Fourth Ave., Seattle, WA, 98101.

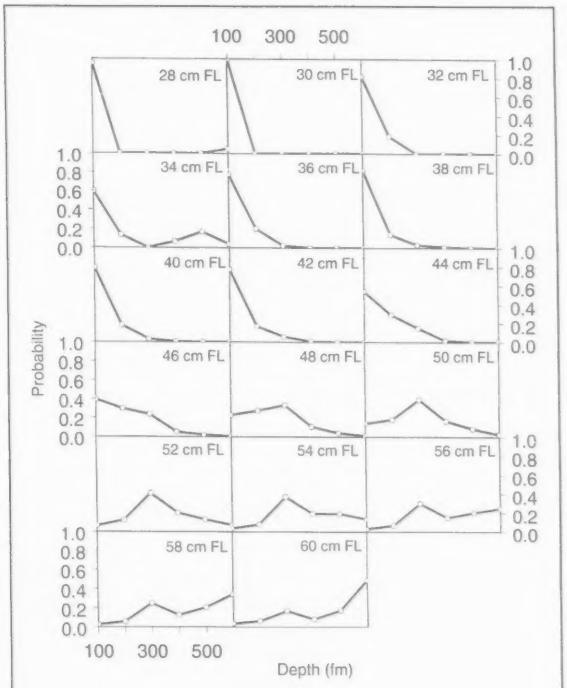


Figure 2

Average depth distributions for sablefish (Table 5) from October to December by length group.

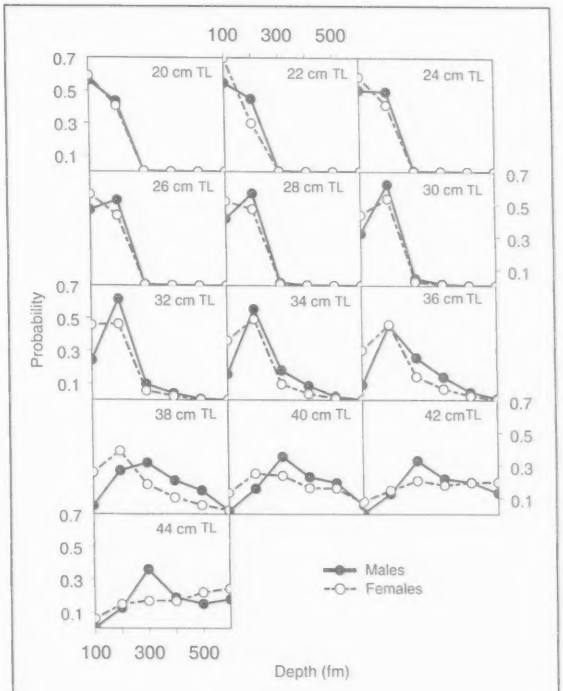


Figure 3

Average depth distributions for male and female Dover sole (Table 6) from October to December by length group.

this and the expression from Equation 8 for $F_{y,d}$ into Equation 7 gives

$$\frac{C_{y,L}}{N_{y,L}} = cV_L \sum_d \frac{E_{y,d}}{A_d} p(d \mid L). \quad (11)$$

The commercial fishery selectivity for fish length L in year y is proportional to $C_{y,L} / N_{y,L}$ in Equation 11 because $C_{y,L} = N_{y,L} F_y s_{y,L}$. Thus, commercial fishery selectivities $s_{y,L}$ were proportional to

$$s_{y,L} \propto V_L \sum_d \frac{E_{y,d}}{A_d} p(d \mid L). \quad (12)$$

Following our convention, we rescaled commercial bottom trawl fishery selectivity estimates from Equation 12 so that the largest was one.

We computed preliminary sex and subarea-specific depth distributions for each species by averaging depth distributions for each sex from bottom trawl surveys in each subarea. Depth distributions for male and female sablefish and thornyheads were similar, but male Dover sole appear to move into deep water at smaller sizes than female Dover sole. There were no clear differences between subareas for any species or sex. We therefore calculated "best estimates" (Tables 5–8; Figs. 2–5) of depth distributions for sablefish and thornyheads by combining subareas and sexes (i.e. by computing survey-specific depth distributions for males and females combined, and then averaging over all surveys). For Dover sole, we calculated sex-specific depth distributions based on combined subareas (i.e. by computing survey-specific depth distributions for males and females separately and then averaging over all surveys). Depth distributions for male and female Dover sole combined (not shown) can be approximated by averaging sex-specific values (e.g. averaging values and rescaling the averages to a maximum of one).

Our best estimates of commercial bottom trawl fishery selectivities for each subarea, year, and species were based on subarea-specific fishing effort data (Tables 1–2) and our best estimates of depth distributions for the whole coast and sexes combined. Preliminary calculations suggested that commercial bottom trawl selectivities for male and female Dover sole were similar (even though depth distributions were different); therefore we combined sexes for final selectivity calculations. Apparently, selectivity calculations for Dover sole were relatively insensitive to differences in depth distributions for males and females because of the overwhelming effects of changes over time in the distribution of commercial fishing effort. Additional data may be required to identify clearly differences in selectivity patterns for male and female Dover sole in the commercial bottom trawl fishery.

Results and discussion

Our best estimates of depth distributions (Tables 5–8; Figs. 2–5) during October–December (when the surveys were conducted) confirm ontogenetic migration patterns of Dover sole (Jacobson and Hunter, 1993), shortspine thornyhead (Jacobson and Vetter, 1995), and sablefish (Parks and Shaw, 1990; Saunders et al., 1997; Sigler et

Table 5

Average depth distributions, i.e. probabilities of depth given length or $p(d|L)$, and CVs for sablefish (sexes combined) between 36°00′N and 48°30′N and between 100 and 699 fm during October–December based on eight National Marine Fisheries Service bottom trawl surveys. The largest and smallest length groups are "plus" groups (i.e. include larger or smaller fish). Length groups (2 cm) are identified by the lower bound (e.g. 30 cm means 30–31.99 cm). For example, the 28-cm group includes all specimens <29.9 cm. Four surveys took sablefish 28–30 cm sablefish, three surveys took 32-cm sablefish, six surveys took 34-cm sablefish, seven surveys took 36-cm sablefish, and all eight surveys took 38–60 cm sablefish. The symbol "—" means that CV could not be calculated because the average depth distribution was zero.

	Depth intervals (fm)					
Fork length (cm)	100–199	200–299	300–399	400–499	500–599	600–699
Depth distributions						
28	0.9506	0.0000	0.0000	0.0000	0.0000	0.0494
30	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
32	0.8150	0.1850	0.0000	0.0000	0.0000	0.0000
34	0.5963	0.1334	0.0000	0.0664	0.1667	0.0372
36	0.7767	0.1999	0.0234	0.0000	0.0000	0.0000
38	0.8191	0.1405	0.0304	0.0090	0.0010	0.0000
40	0.7886	0.1764	0.0303	0.0047	0.0000	0.0000
42	0.7707	0.1654	0.0550	0.0079	0.0000	0.0011
44	0.5380	0.2904	0.1490	0.0174	0.0048	0.0004
46	0.3941	0.2965	0.2361	0.0500	0.0194	0.0040
48	0.2301	0.2761	0.3361	0.1073	0.0401	0.0104
50	0.1421	0.1845	0.3947	0.1685	0.0858	0.0244
52	0.0653	0.1239	0.4071	0.2015	0.1301	0.0722
54	0.0344	0.0784	0.3697	0.1922	0.1908	0.1346
56	0.0300	0.0675	0.3007	0.1509	0.2034	0.2476
58	0.0258	0.0567	0.2464	0.1256	0.2051	0.3404
60	0.0333	0.0614	0.1679	0.0806	0.1719	0.4848
CV						
28	0.05	—	—	—	—	1.00
30	0.00	—	—	—	—	—
32	0.23	1.00	—	—	—	—
34	0.23	0.64	—	1.00	1.00	1.00
36	0.15	0.52	0.96	—	—	—
38	0.09	0.42	0.98	0.73	1.00	—
40	0.12	0.43	0.79	1.00	—	—
42	0.12	0.38	0.64	0.58	—	1.00
44	0.19	0.26	0.54	0.47	0.54	1.00
46	0.19	0.21	0.36	0.22	0.32	0.31
48	0.21	0.22	0.21	0.14	0.13	0.46
50	0.22	0.22	0.11	0.12	0.11	0.24
52	0.23	0.21	0.06	0.13	0.10	0.22
54	0.28	0.22	0.07	0.13	0.11	0.16
56	0.17	0.24	0.09	0.15	0.09	0.13
58	0.26	0.14	0.12	0.14	0.16	0.14
60	0.28	0.11	0.16	0.25	0.13	0.11

al., 1997; Methot et al., 1998). For sablefish, Dover sole and shortspine thornyhead, the smallest individuals were found almost entirely in shallow water (100–199 fm for sablefish and 100–299 fm for Dover sole and shortspine thornyhead). The largest individuals occupied the entire range of depths but were relatively rare in the shallowest water and relatively abundant in the deepest water. As indicated by Jacobson and Vetter (1995), depth distributions showed little evidence of ontogenetic migration in longspine thornyhead (but see below).

Our depth distribution results for Dover sole, like results in Jacobson and Hunter (1993, their Figs. 2–3), show that males 22–32 cm TL were most common at depths of 200–299 fm. Female Dover sole of the same size were more often found in shallower water (100–199 fm). Larger Dover sole (38–44 cm FL) of both sexes were more common in deeper water, where males were most common at 300–399 fm. These patterns seem clear, although, as pointed out by a reviewer, there was substantial overlap in 95% confidence intervals for the depth distributions of male and female Dover sole.

Selectivity patterns for groundfish in the deep-water commercial bottom trawl fishery were complex and dynamic (Figs. 6–9). As expected, there were differences in fishery selectivity estimates for commercial bottom trawls among species, between subareas, and over time (Figs. 6–9). Selectivities for species with strong ontogenetic migration (sablefish, shortspine thornyheads and Dover sole) changed most over time. For these fishes, commercial bottom trawl selectivity curves were dome-shaped with peaks that shifted towards larger sizes in later years as the relative amount of fishing effort increased on deep-water fishing grounds where large fish were most common.

Shifts in commercial bottom trawl selectivity patterns towards larger sizes (Figs. 6–9) were most pronounced in the north because the proportion of total commercial bottom trawl fishing effort in deep water over the continental slope was higher in the southern subarea during the early years of our study than in the northern subarea (Tables 5–6). Higher proportions of total commercial bottom trawl effort in deep water (where large fish are most common) during the early years caused relatively high selectivities for large fish in the southern subarea.

Changes in commercial bottom trawl selectivity patterns over time in sablefish, shortspine thornyhead, and Dover sole (Figs. 6–8) were large enough to be important in stock assessment work (Rogers et al., 1997), particularly if assessments are carried out for northern fishing areas. Most of the changes in selectivity patterns over time were for relatively large fish on the right-hand side of the selectivity curves. Commercial bottom trawl selectivities for smaller fish on the left-hand side of the selectivity

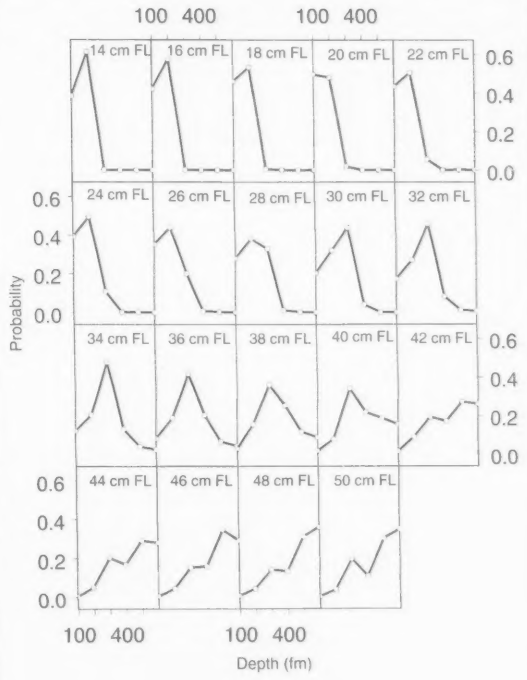


Figure 4

Average depth distributions for shortspine thornyhead (Table 7) from October to December by length group.

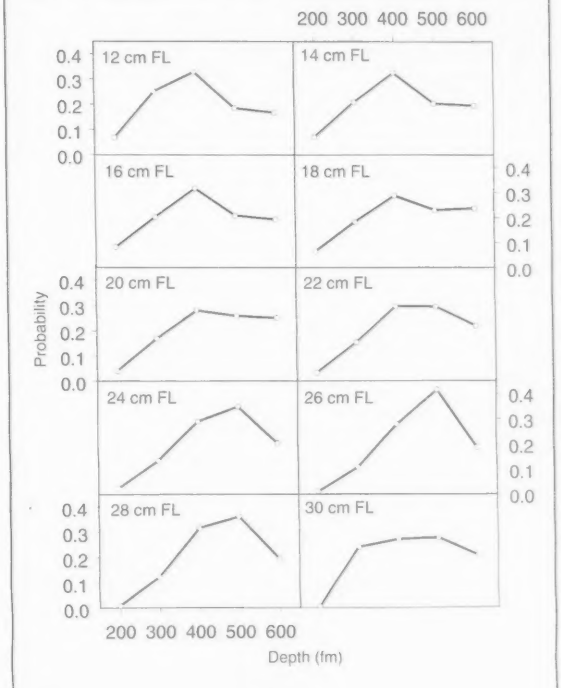


Figure 5

Average depth distributions for longspine thornyhead (Table 8) from October to December by length group.

Table 6

Average depth distributions, i.e. probabilities of depth given length or $p(d \mid L)$, and CVs for male and female Dover sole between 36°00′N and 48°30′N Lat and between 100 and 699 fm during October–December based on eight National Marine Fisheries Service bottom trawl surveys. Length groups and depth intervals defined as in Table 5. All eight surveys took 20–44 cm male and female Dover sole. The symbol "—" means that CV could not be calculated because the average depth distribution was zero.

	Depth intervals (fm)					
Total length (cm)	100–199	200–299	300–399	400–499	500–599	600–699
Depth distributions (males)						
20	0.5616	0.4333	0.0051	0.0000	0.0000	0.0000
22	0.5479	0.4491	0.0031	0.0000	0.0000	0.0000
24	0.5018	0.4928	0.0053	0.0000	0.0000	0.0000
26	0.4652	0.5256	0.0080	0.0010	0.0001	0.0000
28	0.4116	0.5664	0.0185	0.0033	0.0003	0.0000
30	0.3212	0.6225	0.0447	0.0111	0.0006	0.0000
32	0.2412	0.6175	0.0956	0.0392	0.0065	0.0000
34	0.1565	0.5560	0.1802	0.0859	0.0201	0.0014
36	0.0916	0.4552	0.2575	0.1394	0.0472	0.0092
38	0.0506	0.2654	0.3139	0.2052	0.1444	0.0205
40	0.0174	0.1560	0.3527	0.2276	0.1916	0.0548
42	0.0046	0.1248	0.3282	0.2167	0.1951	0.1305
44	0.0041	0.1239	0.3592	0.1859	0.1497	0.1772
CV (males)						
20	0.20	0.27	1.00	—	—	—
22	0.20	0.24	0.87	—	—	—
24	0.16	0.16	0.57	—	—	—
26	0.18	0.15	0.51	0.66	1.00	—
28	0.18	0.13	0.27	0.58	1.00	—
30	0.20	0.10	0.24	0.29	0.57	—
32	0.20	0.08	0.19	0.39	0.43	—
34	0.24	0.09	0.18	0.35	0.40	0.52
36	0.28	0.15	0.19	0.22	0.28	0.33
38	0.36	0.21	0.08	0.18	0.24	0.13
40	0.39	0.33	0.07	0.14	0.21	0.20
42	0.56	0.21	0.07	0.18	0.22	0.25
44	0.66	0.28	0.10	0.22	0.22	0.23

continued

curves resemble the underlying vulnerability curves. These results imply that temporal changes in the right-hand side of the curve should be of greatest concern to stock assessment scientists.

Commercial bottom trawl selectivities for large longspine thornyhead may have increased slightly over time as the fishery moved into deeper water (Fig. 9). This result implies a small amount of ontogenetic migration in longspine thornyhead not evident in our length-specific depth distributions (Fig. 5). Selectivity calculations, which are based on the full suite of depth distributions and fishing effort data, may be a more sensitive indicator of ontogenetic migration patterns not clearly visible in plots showing length-specific depth distributions for longspine thornyhead. It is also possible that the hint of ontogenetic migration in longspine thornyhead was due to estimation errors in depth distributions, lack of species-specific vulnerability parameters, or other factors.

As described above, differences between sexes in length-specific commercial bottom trawl selectivities were minor. This implies little need for sex-specific selectivity parameters in stock assessment models if selectivity is calculated as a function of length. If selectivity is modeled as a function of age, and growth rates of males and females are different (often the case for west coast groundfish), then sex-specific selectivity parameters may be required. Sex-specific length-based selectivity parameters would be required if ontogenetic migration is more closely related to age than length.

Clear trends in our fishery selectivity estimates for commercial bottom trawls suggest a reasonable level of preci-

Table 6 (continued)

	Depth intervals (fm)					
Total length (cm)	100–199	200–299	300–399	400–499	500–599	600–699
Depth distributions (females)						
20	0.5897	0.4066	0.0037	0.0000	0.0000	0.0000
22	0.6982	0.2988	0.0030	0.0000	0.0000	0.0000
24	0.5842	0.4119	0.0016	0.0022	0.0000	0.0000
26	0.5609	0.4304	0.0068	0.0019	0.0000	0.0000
28	0.5189	0.4687	0.0100	0.0025	0.0000	0.0000
30	0.4331	0.5347	0.0248	0.0075	0.0000	0.0000
32	0.4580	0.4632	0.0549	0.0217	0.0020	0.0002
34	0.3635	0.4930	0.0967	0.0375	0.0079	0.0015
36	0.3025	0.4605	0.1421	0.0670	0.0241	0.0038
38	0.2540	0.3860	0.1811	0.1006	0.0550	0.0235
40	0.1294	0.2488	0.2352	0.1598	0.1578	0.0691
42	0.0800	0.1455	0.2052	0.1784	0.1934	0.1975
44	0.0580	0.1481	0.1680	0.1662	0.2185	0.2412
CV (females)						
20	0.27	0.40	0.74	—	—	—
22	0.18	0.41	1.00	—	—	—
24	0.17	0.25	0.65	0.80	—	—
26	0.15	0.19	0.49	0.64	—	—
28	0.13	0.13	0.71	0.35	—	—
30	0.19	0.16	0.40	0.32	—	—
32	0.15	0.14	0.25	0.22	0.60	1.00
34	0.19	0.16	0.32	0.26	0.48	0.73
36	0.19	0.14	0.27	0.24	0.37	0.73
38	0.20	0.17	0.21	0.19	0.23	0.32
40	0.31	0.14	0.15	0.19	0.39	0.24
42	0.26	0.13	0.15	0.14	0.25	0.20
44	0.30	0.20	0.10	0.14	0.20	0.14

sion (see below for a discussion of possible bias). A simple approach to measuring precision would be to fit smooth lines to the estimates and calculate variation of the residuals. Variances might also be computed analytically, on the variance of depth distributions, or by bootstrapping (Efron, 1982).

Depth distributions and commercial bottom trawl selectivities could be estimated from surveys with different types of survey bottom trawls because the selectivity of the survey gear cancels out in estimation of depth distributions for the population. It is important, however, not to simply pool survey data collected with different types of trawls. Estimates of depth distribution from individual surveys $^{s}p(d \mid L)$ should be averaged or combined instead.

Our methods could be used to calculate depth distributions and commercial bottom trawl selectivities as a function of age if sufficient age data from bottom trawl surveys were available. In fact, the approach could be extended to include both length and age simultaneously. This procedure might be useful for species such as sablefish, where the relationship between age, length, and depth is complex (Norris, 1997; Methot et al., 1998). In the absence of survey age data, an inverted von Bertalanffy growth model could be used to convert selectivities for commercial fishing based on length to selectivities based on age.

Our approach to estimating fishery selectivities complements traditional approaches using stock assessment models because our assumptions were different. In particular, our approach did not involve assumptions about relationships between fish size and natural mortality that were made either implicitly (natural mortality assumed constant for all size groups) or explicitly (e.g. Tagart, et al., 1997) in most stock assessment models. As described above, size-dependent natural mortality rates and size-dependent fishery selectivities tended to be confounded in fishery length-composition or age-composition data (e.g. Tagart et al., 1997). It is possible that estimates of fishery selectivity for commercial bottom trawls might be useful in stock assessment models as a basis for estimating trends in length-specific natural mortality. Another approach would be to use estimates of fishery selectivity from our method

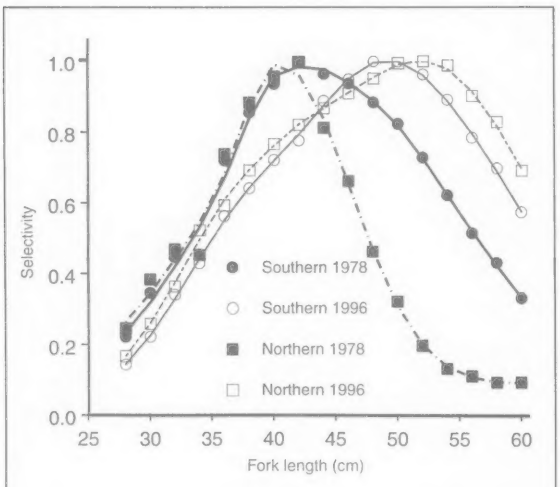


Figure 6

Commercial bottom trawl (4 1/2-inch mesh codend) fishery selectivity estimates for sablefish (sexes combined) in the northern and southern subareas during 1978 and 1996. Selectivity curves for other years were intermediate. Estimates for 1978 are biased owing to commercial trawls in the fishery with smaller mesh codends. Smooth lines show trends and were fitted to estimates by locally weighted regression smoothing (LOESS).

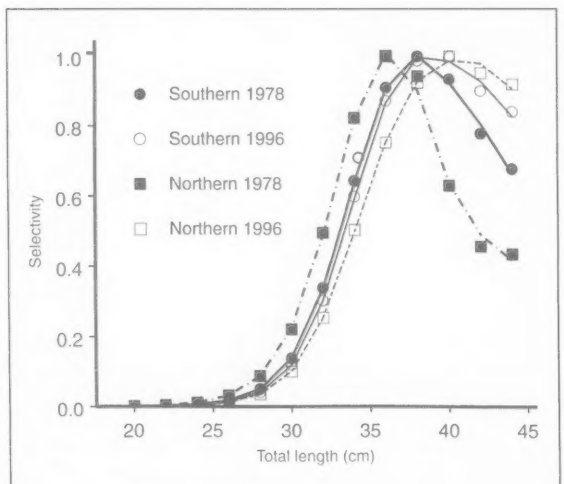


Figure 7

Commercial bottom trawl (4 1/2-inch mesh codend) fishery selectivity estimates for Dover sole (sexes combined) in the northern and southern subareas during 1978 and 1996. Selectivity curves for other years were intermediate. Estimates for 1978 are biased due to commercial trawls in the fishery with smaller mesh codends. Smooth lines show trends and were fitted to estimates by locally weighted regression smoothing (LOESS).

as Bayesian priors for selectivity parameters estimated by stock assessment models (Methot, 1990).

Our estimates of depth distributions reflect conditions during the autumn (October–December). Our study did not include data collected during other seasons that could be used to test hypotheses about seasonal migrations between deep and shallow water (Alverson, 1960). Additional bottom trawl survey data collected at different times of the year with a variety of vessels and trawl gears are available (Lauth[3]) and could be used to measure seasonal differences in depth distributions.

Our analysis used data from bottom trawl surveys to estimate depth distributions. Our approach might be applicable to other types of surveys as long as densities of organisms in each strata can be calculated on an relative or absolute basis. Although survey gear selectivities cancel out in calculations, it is important that the survey gear be relatively efficient for length groups used in calculations. Otherwise, density estimates used to calculate depth distributions may be too variable.

The assumption that survey bottom trawl selectivities are constant with depth is important in calculating depth distributions $p(d \mid L)$ because the proof that survey selectivities cancel out depends on the assumption. It is possible for example, that small fish might evade bottom trawls by hiding in rubble or depressions. If there were more rubble or depressions in deep water than in shallow water, then bottom trawl survey selectivities would change with depth, and depth distribution estimates (as well as commercial fishery bottom trawl selectivity calculations) would be affected. The magnitude of any possible problem would depend on a variety of factors (e.g. the relative abundance of small fish at depths with more or less rubble) and cannot be predicted in general. However, factors that affect selectivity of survey bottom trawls (including herding, escapement under the footrope, escapement over the top of the net, and escapement through meshes) are not important in calculating depth distributions, even if they depend on fish size, as long as they remain the same for all depth strata.

Sensitivity of selectivity estimates to errors in fishing effort data

Our estimator for fishery selectivities does not depend on knowing total effective commercial fishing effort ($E_{y,d}$) for each depth stratum. It does depend on knowing the proportion of total effective fishing effort (which is proportional to fishing mortality) in each stratum. This means that unreported fishing effort would not affect our calculations unless there were differences in depth of fishing among fishermen who did and did not turn in log data, differences among states in depth of fishing and proportion of fishermen who submit log data, or differences in logbook reporting rates among fishermen who fish in different areas or at different depths.

[3] Lauth, R. 1998. Personal commun. Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way, BIN C15700, Seattle, WA 98115-0070.

Our approach to calculating fishery selectivities for commercial bottom trawls is based on the assumption that nominal fishing effort data in each stratum from logbooks is a relative measure of commercial fishing mortality. Bias in fishing effort data as a measure of relative fishing mortality (e.g. due to differences among depth strata in average fishing power) would affect our estimates of fishery selectivities for commercial bottom trawls. It would be better to use a standardized measure of fishing effort for each stratum adjusted for differences in season, gear, vessel size, engine size, skipper skill, target species, bycatch, or other operational characteristics of the vessels (Hilborn and Walters, 1992). We hypothesize that this is a minor problem in interpretation of our results, however, because the nominal fishing effort data we used showed clear and substantial shifts towards deep water (Tables 1–2).

Sensitivity of selectivity estimates to vulnerability estimates from field studies

Vulnerability estimates were the most important uncertainty in our estimates of fishery selectivities for commercial bottom trawls (but did not affect estimates of depth distributions because they were not used to calculate depth distributions). We conducted extensive sensitivity analysis for each species and determined that a 1-cm change in the assumed length at 50% vulnerability (L_{50} in Table 4) shifted the commercial bottom trawl selectivity curves in the same direction by about 1 cm.

The vulnerability parameters used in our analysis were for 4½-inch mesh which is the current legal minimum mesh size in bottom trawls along the west coast, but smaller mesh was used by some vessels during earlier years (Pacific Fishery Management Council, 1998). Changes over time in commercial mesh size would affect our calculations for early years and small fish. The extent of the potential problem is unknown because no vulnerability parameters were available for small mesh gear (e.g. 3-inch mesh) and because there is no information about proportions of total fishing effort by trawls with different mesh size during early years. The potential problem is not important in estimating selectivity of commercial bottom trawls during recent years because recent mesh size regulations make 4½-inch mesh standard in the fishery.

Results from Perez-Comas (1996) were valid estimates of selectivities (as defined in his study) but likely underestimate vulnerability (as defined in our analysis) and bias our estimates for small fish. Precise definition of terms is important in this regard.

According to Perez-Comas (1996), his estimates measured "the differential retention of certain sizes of fish after they come in contact with the gear" (Gulland, 1983). In our words, Perez-Comas measured "the relative probability of capture given that a fish entered the mouth of the trawl." These definitions are similar but not identical to our definition of vulnerabilities as "the relative probability of capture given that a fish is in the path of the trawl." In particular, Perez-Comas's (1996) definition differs from ours to the extent that fish of different sizes have different probabilities of moving

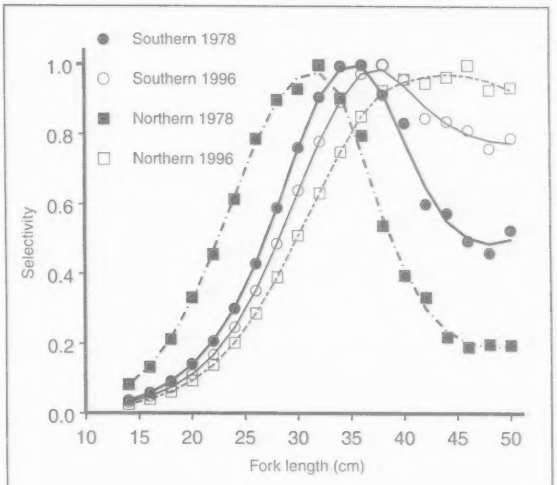


Figure 8

Commercial bottom trawl (4½-inch mesh codend) fishery selectivity estimates for shortspine thornyhead (sexes combined) in the northern and southern subareas during 1978 and 1996. Selectivity curves for other years were intermediate. Estimates for 1978 are biased owing to commercial trawls in the fishery with smaller mesh codends. Smooth lines show trends and were fitted to estimates by locally weighted regression smoothing (LOESS).

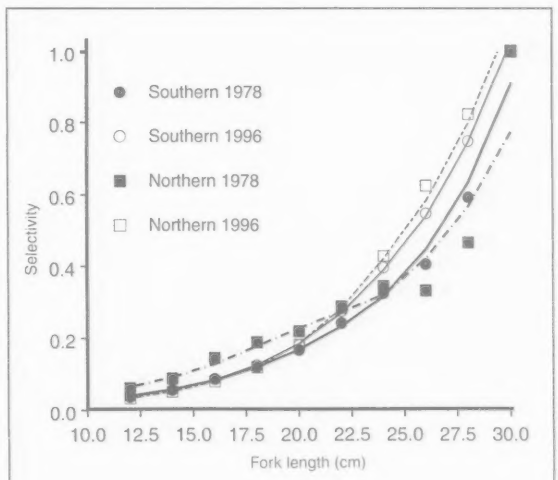


Figure 9

Commercial bottom trawl (4½-inch mesh codend) fishery selectivity estimates for sablefish (sexes combined) in the northern and southern subareas during 1978 and 1996. Selectivity curves for other years were intermediate. Estimates for 1978 are biased owing to commercial trawls in the fishery with smaller mesh codends. Smooth lines show trends and were fitted to estimates by locally weighted regression smoothing (LOESS).

away from or into the path of the net and to the extent that escape after entering the net depends on fish size.

Perez-Comas (1996) used a sophisticated estimation procedure but, conceptually, his vulnerability estimates were proportional to the length-specific ratios of catch rates in 4½-inch and 3-inch mesh (i.e. V_L proportional to C_L/K_L, where C_L and K_L are catch rates with 4½ and 3-inch gear). It is likely that catch rates for small fish in 3-inch mesh

Table 7

Average depth distributions, i.e. probabilities of depth given length or $p(d \mid L)$, and CVs for shortspine thornyhead (sexes combined) between 36°00′N and 48°30′N lat and between 100 and 699 fm during October–December based on eight National Marine Fisheries Service bottom trawl surveys. Length groups and depth intervals defined as in Table 5. All eight surveys took 14–50 cm shortspine thornyhead. The symbol "—" means that the CV could not be calculated because the average depth distribution was zero.

	Depth intervals (fm)					
Fork length (cm)	100–199	200–299	300–399	400–499	500–599	600–699
Depth distributions						
14	0.3863	0.6127	0.0011	0.0000	0.0000	0.0000
16	0.4221	0.5752	0.0027	0.0000	0.0000	0.0000
18	0.4607	0.5330	0.0061	0.0000	0.0003	0.0000
20	0.4969	0.4816	0.0185	0.0006	0.0024	0.0000
22	0.4349	0.5056	0.0567	0.0002	0.0025	0.0002
24	0.3920	0.4944	0.1079	0.0028	0.0025	0.0006
26	0.3506	0.4383	0.1989	0.0075	0.0028	0.0019
28	0.2780	0.3779	0.3271	0.0117	0.0032	0.0021
30	0.2011	0.3174	0.4373	0.0405	0.0020	0.0016
32	0.1718	0.2694	0.4564	0.0824	0.0130	0.0070
34	0.1214	0.2042	0.4773	0.1309	0.0404	0.0259
36	0.0826	0.1874	0.4169	0.2025	0.0662	0.0445
38	0.0291	0.1544	0.3592	0.2522	0.1168	0.0884
40	0.0190	0.0797	0.3410	0.2175	0.1868	0.1560
42	0.0164	0.0906	0.1919	0.1709	0.2713	0.2589
44	0.0039	0.0518	0.2034	0.1698	0.2908	0.2804
46	0.0056	0.0437	0.1539	0.1608	0.3453	0.2907
48	0.0080	0.0440	0.1429	0.1342	0.3108	0.3602
50	0.0034	0.0386	0.1970	0.1095	0.3033	0.3482
CV						
14	0.18	0.11	0.45	—	—	—
16	0.14	0.10	0.44	—	—	—
18	0.06	0.05	0.25	—	1.00	—
20	0.08	0.08	0.26	0.45	0.91	—
22	0.09	0.07	0.25	0.66	1.00	1.00
24	0.10	0.06	0.21	0.27	0.76	0.74
26	0.11	0.09	0.11	0.15	0.43	0.65
28	0.10	0.07	0.03	0.20	0.75	0.52
30	0.12	0.07	0.04	0.22	0.67	0.69
32	0.15	0.08	0.05	0.17	0.31	0.35
34	0.19	0.14	0.09	0.14	0.23	0.59
36	0.18	0.16	0.10	0.12	0.34	0.27
38	0.23	0.21	0.10	0.13	0.27	0.25
40	0.43	0.23	0.12	0.09	0.11	0.17
42	0.57	0.25	0.15	0.17	0.11	0.17
44	0.69	0.11	0.12	0.15	0.11	0.13
46	0.66	0.28	0.13	0.16	0.07	0.12
48	0.41	0.26	0.18	0.15	0.11	0.09
50	0.46	0.26	0.15	0.12	0.08	0.13

(K_L) were reduced by escapement of small fish through 3-inch meshes so that vulnerabilities estimates for small fish were biased high as well. The extent of the potential bias is unknown but bias was probably low for large fish.

It might be possible to refine estimates of vulnerability parameters by carrying out field studies similar to those analyzed by Perez-Comas, but by using small mesh liners in the codends of commercial bottom trawls as the reference standard. Small mesh can cause problems under commercial fishing conditions (Erickson et al., 1996) and it might therefore be preferable to use codend covers to capture small fish as they escape through codends with commercial-size mesh instead.

As described above, fish may move away from or into the path of a commercial bottom trawl (herding) to an extent that depends on size (Gunderson, 1993). Herding is complex and depends on net design, size, towing speed, and other factors (Ramm and Xiao, 1995). These variables would affect our calculations of size-specific selectivities in commercial bottom trawls to the extent that the vulnerability estimates used in our study would fail to measure the relatively probability of capture for fish of different size in front of commercial bottom trawls. We have little information on this topic for west coast groundfish.

Loss of small fish through 3-inch codends during the paired bottom trawl experiments used to estimate vulnerabilities likely biased our estimates of bottom trawl selectivities in commercial fisheries. Length-composition data for sablefish, Dover sole, and thornyheads from commercial gear with 3-inch codends include fewer small fish than length-composition data from survey bottom trawls with small mesh (3.2 cm) liners (Lauth[3]). We have no other information about size-specific probabilities of escape of small fish, but studies with survey bottom trawls and a variety of species (e.g. Engås and Godø, 1989a; 1989b; Walsh, 1992) show that small fish do escape. We recommend field studies with commercial bottom trawls and video equipment.

Acknowledgments

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Table 8

Average depth distributions, i.e. probabilities of depth given length or $p(d \mid L)$, and CVs for longspine thornyhead (sexes combined) between 36°00′N and 48°30′N lat and between 200 and 699 fm (longspine thornyhead were seldom taken at 100–199 fm) during October–December based on eight National Marine Fisheries Service bottom trawl surveys. Length groups and depth intervals defined as in Table 5. All eight surveys took 12–30 cm longspine thornyhead.

	Depth intervals (fm)				
Fork length (cm)	200–299	300–399	400–499	500–599	600–699
Depth distributions					
12	0.0684	0.2512	0.3288	0.1845	0.1671
14	0.0701	0.2082	0.3252	0.2028	0.1938
16	0.0817	0.2024	0.3155	0.2078	0.1925
18	0.0652	0.1831	0.2875	0.2289	0.2353
20	0.0401	0.1701	0.2801	0.2590	0.2509
22	0.0334	0.1545	0.2970	0.2957	0.2195
24	0.0250	0.1344	0.2894	0.3488	0.2024
26	0.0112	0.1081	0.2784	0.4152	0.1871
28	0.0080	0.1225	0.3151	0.3610	0.1934
30	0.0034	0.2403	0.2711	0.2777	0.2076
CV					
12	0.34	0.09	0.09	0.07	0.09
14	0.38	0.11	0.13	0.09	0.13
16	0.37	0.14	0.10	0.12	0.13
18	0.33	0.14	0.09	0.10	0.11
20	0.25	0.12	0.09	0.11	0.11
22	0.27	0.13	0.07	0.07	0.13
24	0.34	0.09	0.06	0.04	0.14
26	0.26	0.13	0.08	0.03	0.17
28	0.69	0.15	0.15	0.07	0.23
30	0.46	0.19	0.23	0.16	0.25

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Yield-per-recruit analysis for black drum, *Pogonias cromis*, along the East Coast of the United States and management strategies for Chesapeake Bay

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Abstract—Black drum, *Pogonias cromis*, along the U.S. East Coast is subject to commercial and recreational harvest. However, prior to this study no modeling had been undertaken to examine the potential for overfishing in the Chesapeake Bay region. We present evidence from yield-per-recruit models that growth overfishing of black drum is unlikely under current fishing practices in this region. Particular attention was given to fishing practices in the Chesapeake Bay region where old, large fish predominate in the commercial and recreational catches (mean age=26 years; mean total length=108.4 cm; mean weight 22.1 kg). Yield-per-recruit model results showed that growth overfishing was unlikely in the Chesapeake Bay region under all but the lowest estimates of natural mortality (M=0.02–0.04). Such extreme low values of M predict potential life spans of 200 years and were dismissed as improbable—the oldest age recorded for this species is 59 years. Additionally, biomass-per-recruit model results indicated a 42–59% decrease to current biomass from the unfished stock. The apparent age-specific migration of this stock argues for protection of young fish that have dominated the catch in Northeast Florida. Modeling indicated that growth overfishing could result from heavy fishing on these young ages and would all but eliminate this resource of the northern fishery.

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Black drum (*Pogonias cromis*; family Sciaenidae) range in U.S. waters primarily from Massachusetts to Florida along the East Coast and, in the Gulf of Mexico, from the west coast of Florida along the northern Gulf to Texas. They form at least three populations, at least two in the Gulf of Mexico (Gold et al., 1995) and one along the U.S. East Coast (Gold and Richardson, 1998; Gold[1]). This population structure is seen as "isolation by distance" (Gold and Richardson, 1998). East Coast black drum undertake long-range migrations with a general pattern of movement to the north and inshore in spring, and south and offshore in the fall (Richards, 1973; Murphy and Taylor, 1989; Jones and Wells, 1998). These seasonal migrations are age-specific and influence exploitation patterns differently along the coast. Although the East Coast stock shows a maximum age of 59 years, which indicates low total annual mortality of 8–11% (Jones and Wells, 1998), a greater proportion of old fish are found north of Cape Hatteras, and the potential exists for different age-specific mortalities along the range. Along the East Coast, fisheries for black drum predominantly target small, young fish in the south (Music and Pafford, 1984; Murphy and Muller[2] and Wenner[3]) and large, old fish in the north (Jones and Wells, 1998). Although small fish are targeted in the south, large fish are present and are caught occasionally in the recreational fisheries there. In contrast, small fish are rarely present north of Cape Hatteras besides young of the year fish that leave the bays after their first summer. Hence, little fishing mortality occurs to young fish in the northern part of the range.

Compared with other exploited sciaenids, black drum do not support large recreational or commercial fisheries. Along the East Coast between 1979 and 1994, commercial catches averaged only 99,510 kg yearly (218,923 pounds)[2,4,5,6,7,8] Virginia and Florida have the greatest average annual land-

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footnote continued on next page

ings (averaging 37,000 and 26,000 kg respectively), whereas New Jersey, Delaware, Maryland, North Carolina, South Carolina, and Georgia have average landings of less than 18,000 kg. In contrast, between 1981 and 1994 recreational landings averaged 315,000 kg (693,000 pounds)[2,9] annually, 300% higher than the commercial catch. Recreational landings north of Cape Hatteras vary from 0.4% to 78% of the annual East Coast recreational catch, reflecting variations in abundance of older fish and in their seasonal migration patterns.

With its location at the northern end of the range, Chesapeake Bay fisheries target black drum that are primarily old (26 yr), and large (108.4 cm; 22.1 kg) during a short season; most of the catches occur from April to June (Jones and Wells, 1998). Large fish enter the Bay in April and are caught by the commercial fishery with 33-cm stretch mesh anchored and drifted gill nets. Historically, the commercial market is local, and fillets and roe are a spring treat for residents of the eastern shore of Virginia and Maryland during April and May (Jones et al., 1990). Because of this limited market that becomes saturated, the price drops in late spring and commercial fishermen turn from black drum to pursue more profitable fishes. The recreational fishery usually begins and ends a month later than the commercial fishery, from May to June, and anglers target large trophy fish with hook and line. Although the recreational season is short, it occurs before more popular fish enter the Bay, and the fishery supports local business at that time. Thus, the black drum fishery is important to the economies of two of the poorest counties in Virginia, which are located on the eastern shore (Jones et al., 1990).

In the mid-Atlantic region, the lack of accurate catch and effort data from the commercial and recreational black drum fisheries makes it difficult to evaluate whether the long-term fluctuations in population abundance and the current decline in abundance of citation-size fish result from natural patterns of dominant year classes or from excess exploitation and subsequent population decline. Reports of catch and effort in the commercial fishery have been based, generally, on voluntary reporting. Likewise, the difficulty in sampling this short-season and charter-based recreational fishery has led to estimates of catch and effort that are characterized by extremely broad confidence limits. Even so, in response to the concerns of Virginia's recreational anglers to supposed population decline, commercial harvest quotas were imposed on these fisheries in 1992 in the absence of any stock assessment (Commonwealth of Virginia, 1992, VMRC regulation 4 VAC 20-320-10 et seq.).

Yield-per-recruit models can provide the benchmarks for assessing growth overfishing (Gulland, 1983; King, 1995). Specifically, yield-per-recruit modeling provides reference points to theoretically maximize yield from a cohort (F_{MAX}), or increase the number of trophy-size fish in the population. Because F_{MAX} frequently results in unsustainable harvests, an *ad hoc* benchmark ($F_{0.1}$) is calculated to provide more conservative harvest recommendations. However as important as this modeling is to science-based management, no published application of yield-per-recuit models exists for black drum from the Chesapeake Bay region. In our study we used data from Chesapeake Bay (Jones and Wells, 1998) and Florida (Murphy and Taylor, 1989) to evaluate the effect of fishing mortality and age at first capture on yield-per-recruit models of these fish, especially for management in the Bay. Although more accurate stock assessments result when catch-age or age-structured models such as ADAPT are used, the absence of a time series of aged-catch data precludes their use for this fishery. Until such data become available, the results of yield-per-recruit models can be used now to determine whether regulations such as size limits, catch quotas, and effort limitations, which are already in effect, are necessary to manage this fishery.

Materials and methods

Yield-per-recruit analysis

The Beverton-Holt yield-per-recruit model (Beverton and Holt, 1957) was used to calculate yield-per-recruit curves following the formula

$$Y/R = Fe^{-M(t_c - t_r)} W_\infty \sum_{n=0}^{3} \frac{U_n e^{-nK(t_c - t_0)}}{F + M + nK}, \quad (1)$$

where Y/R = yield-per-recruit in weight (kg);
F = instantaneous fishing mortality coefficient;
M = instantaneous natural mortality coefficient;
U_n = summation parameter (U_0=1, U_1=–3, U_2=3, U_3=–1);
t_c = mean age (years) at first capture;
t_r = mean age (years) at recruitment to the fishing area; and
W_∞ = asymptotic weight;
t_0 = hypothetical age the fish would be zero length; and
K = the Brody growth coefficient.

Computations were performed by using a modification of the computer program *B-H3* available in the Basic Fisheries Science Programs package (Saila et al., 1988). Parameters used in these simulations are summarized in Table 1. The first two parameters, t_0 and K, are derived from the von Bertalanffy growth equation for black drum (Jones and Wells, 1998):

$$l_t = 117.3\left(1 - e^{-0.105(t+2.3)}\right). \quad (2)$$

Because fish aged 1–5 were not available in Chesapeake Bay, our estimate of K (0.105) was smaller than that obtained by

[7] (*continued*) Coastal Resources Division, One Conservation Way, Brunswick, GA 31523-8600.

[8] Sutherland, D. 1995. 1979–94 Black drum commercial landings for Atlantic Coast states. Fisheries Statistics Division, National Marine Fisheries Service, 1315 East West Highway, Silver Spring, MD 20910.

[9] Fisheries Statistics Division and Economics Division. 1996. Personal commun. Fisheries Statistics Div. and Economics Div., National Marine Fisheries Service, 1315 East West Highway, Silver Spring, MD 20910.

Murphy and Taylor, (K=0.124; 1989) for black drum sampled from the northeast coast of Florida. Hence, we also used estimates of K from the northeast coast of Florida in our modeling to ensure that results would reflect the available scientific data from the U.S. East Coast. For both areas, asymptotic mean weight, W_∞, was converted from an allometric weight-length relationship (b=3.11; Jones and Wells, 1998). This slight deviation from isometric growth (b=3.0) may result in a small overestimation of yield (less than 7%) which Ricker (1975) dismissed as inconsequential to further calculations. Because we focused on the relative yields that result from varying t_0 and F at different levels of M, differences in yield should be even less than this absolute level (Barbieri et al., 1997).

Table 1

Parameter estimates or range of values used in yield-per-recruit and biomass simulations for black drum, *Pogonias cromis*, on the east coast of the U.S. Data taken from Jones and Wells (1998) for the Chesapeake Bay and Murphy and Taylor (1989).

Parameter	Chesapeake Bay	NE Florida	Method
t_c	5–25 yr		age composition of catches
t_r	5 yr	1 yr	life history information
t_0	–2.3 yr	–1.3 yr	growth curve
K	0.105 yr	0.124 yr	growth curve
L_∞	117.3 cm	117.2 cm	growth curve
W_∞	27.5 kg	25.5 kg	converted from L_∞
Z	0.08–0.12		catch curves and longevity
M	0.00–0.12		longevity
β	3.11		length-weight regression

Age of recruitment to the fishing area, t_r, was unknown for this fishery and was set to age 1 for the Florida fishery and age 5 for the Chesapeake Bay fishery, a year less than the youngest adult black drum caught in the Bay during our three-year study. Fisheries-based data included Z, F, M, and t_c. Estimates of the instantaneous total mortality, Z, for fully recruited black drum were obtained from catch-curve analysis and maximum age procedures, and ranged from 0.08 to 0.12 (Murphy and Taylor, 1989; Jones and Wells, 1998). Although we had direct estimates of total mortality, Z, we lacked independent estimates of instantaneous fishing mortality, F, and instantaneous natural mortality, M. However, the estimate of Z allowed us to estimate current levels of fishing mortality, $F_{CUR(i)}$, for different values of M, as

$$F_{CUR(i)} = Z - M_i, \tag{3}$$

where M_i = 0.02–0.12.

We estimated the most probable value of M by extrapolating to maximum age estimates realistic for an unfished fishery. This range of M was lower than that predicted with a multiple regression developed by Pauly (1980; M=0.16–0.30). Using our lower estimate of M, we made our modeling more sensitive to potential growth overfishing; therefore management strategies would be conservative.

Ricker yield model

Ricker's yield model is used to simulate the potential for growth overfishing over the life of a cohort by measuring available biomass at age under various levels of F (King, 1995). Mortality and growth are opposing effects that result in a maximum biomass during the lifetime at the age of maximum biomass, $t_{CRITICAL}$. The model equation is from Saila et al. (1988):

$$\hat{Y}_c = \sum_{t=t_r}^{t_L} \frac{F_t B_t \left[1 + e^{(G_t - Z_t)}\right]}{2}, \tag{4}$$

where $\hat{Y}_c$ = estimated lifetime equilibrium yield referenced to an arbitrary recruitment biomass of 1000 g;
B_t = biomass at age;
F_t = instantaneous fishing mortality at age;
Z_t = total mortality at age;
G_t = growth in weight-at-age; and
t_i = age where t_i is calculated from the age of first capture, t_c, to the last fishable age, t_L.

When calculated at F=0, the model produces estimates of equilibrium yield for the unfished stock. Computations were performed by using the computer program *Ricker* modified from the Basic Fisheries Science Programs package (Saila et al., 1988).

Parameter values used in simulations are summarized in Table 1. Estimates of growth parameters B_t, and G_t for Chesapeake Bay and Florida black drum were obtained from Jones and Wells (1998) and Murphy and Taylor (1989). Because of the long life of black drum, we grouped parameters into 5-year intervals to increase computation efficiency. Simulations used six values of M (0.02, 0.04, 0.06, 0.08, 0.10, and 0.12) and six levels of F (0.0, 0.02, 0.04, 0.06, 0.08, and 0.10). This model is not used to calculate optimum yield as is the Beverton-Holt yield-per-recruit model. By integrating the area under the curves, reduction in stock biomass at a given level of F can be compared with biomass of the unfished stock, thus demonstrating the loss of trophy-size fish that are prized in recreational fisheries.

Simulations were done to model two scenarios of fishing mortality and their effect on biomass: 1) uniform low F over the life span, and 2) very high F in the first 5-year interval and uniform low F over the remaining lifetime. In the first scenario the chosen level of F was partitioned equally over 12 age intervals. (Because we lacked age-specific estimates of F, the most straightforward approach was to equally partition F across age intervals.) In the second scenario fish in the first 5-year interval were given an F=2.0 and thereafter experienced the chosen level of F

partitioned equally over the remaining 11 age intervals. Hence, in the second scenario the lifetime Z was greater than 2.0. The second scenario was chosen to model extremely severe F on young fish that could be experienced from both directed fisheries and bycatch where young fish predominate.

Cohort biomass and harvesting time

The maximum possible yield for a year class occurs at the age ($t_{CRITICAL}$) when the biomass of the cohort is at its maximum in the absence of fishing. For comparison with the Beverton-Holt and Ricker yield-per-recruit modeling results, we estimated $t_{CRITICAL}$ for black drum following Quinn and Deriso (1999) with the following equation:

$$t_{CRITICAL} = t_0 + \frac{1}{K}\ln\left(1+\frac{\beta}{m}\right), \quad (5)$$

where m = M/K,
β = the length-weight allometry coefficient, and
t_0, K, and M are defined as in Equation 1.

Parameter estimates or the range of values used in calculations are listed in Table 1. Age at maximum biomass can be compared to mean age in the catch to indicate whether further juvenesence is possible.

To calculate the proportion of potential growth span (P_g) remaining when black drum enter the exploited phase of life (Beverton and Holt, 1957), we used the quantity (Beverton, 1963):

$$P_g = (1 - l_c / L_\infty), \quad (6)$$

where L_∞, the asymptotic length, was obtained from Jones and Wells (1998); and l_c, the average length at first capture, was obtained by converting t_c to length with the von Bertalanffy growth curve reported for black drum in Chesapeake Bay (Jones and Wells, 1998) and Florida (Murphy and Taylor, 1989). Both parameters are based on total length in cm.

Results

Modeling with parameters from Chesapeake Bay

Yield-per-recruit curves on F showed that the yield of black drum in Chesapeake Bay could be maximized by decreasing t_c to 10–15 yr over most of the range of M (0.06–0.12) and F used in our simulations (Fig. 1; Table 2). The gains in yield-per-recruit could be substantial. For example, at the estimated current levels of fishing mortality for black drum in Chesapeake Bay (F_{CUR}=0.04–0.06), yields could be increased 58% at M=0.06 and 89% at M=0.08 by decreasing current t_c from 25 yr to 15 yr.

Yield-per-recruit curves showed marked peaks only at the lowest levels of M (0.02; 0.04) when $t_c \leq 10$–15 or at higher levels of M when $t_c \leq 10$ (Fig. 1). Otherwise, curves were asymptotic or rising, and F_{MAX} was reached only at the highest fishing mortalities (F_{MAX}>2.0; Table 2). When M was 0.02, curves peaked for t_c up to 20 yr, resulting in F_{MAX} <0.4. However, because an M of 0.02 predicts a maximum age of over 200 yr in an unexploited stock and because there is no indication of such longevity in black drum, we rejected this scenario as improbable. When M was 0.04, curves peaked for $t_c \leq 15$, for ages constituting less than five percent of the catch and well below the mean age (25 y) in the catch in the Chesapeake Bay fishery. At higher values of M when $t_c \geq 10$, curves were asymptotic or rising and F_{MAX} occurred only at the highest levels of F. Although yields increased continuously with F for M>0.04, increases in yield beyond F=0.1–0.3 were very small.

For $M \geq 0.06$ and $t_c \geq 5$, estimates of F_{CUR} were below the levels giving maximum potential yield-per-recruit (F_{MAX}) and $F_{0.1}$ (Fig. 1; Table 2). For M=0.06, F_{CUR} equals 0.06 at most and $F_{0.1}$ equals 0.07, indicating that, although below the maximum potential yield-per-recruit, estimated current levels of harvest are only slightly below this more conservative benchmark of F. When M>0.06, $F_{0.1}$ is greater than 0.08 and always above F_{CUR}, indicating that current levels of harvest are below this conservative benchmark. In contrast, if $M \leq 0.04$ and $t_c \leq 10$, $F_{0.1}$ is higher than F_{CUR} (Table 2) indicating that there is some justification for decreasing F. However, as mentioned previously, we believe these levels of $M \leq 0.04$ to be unrealistically low for this species.

Curves of biomass on age showed that biomass decreased with increases in M or F (Table 3). Lifetime cohort biomass of an unfished stock decreased by 85% from M=0.02 to M=0.12. Within a given M, increased F resulted in decreased lifetime cohort biomass. For example, when the most credible combinations of M and F_{CUR} were modeled (M=0.06, F_{CUR}=0.06; M=0.08, F_{CUR} = 0.04), biomass declined 59% and 42%, respectively, from that of the unfished stock (Fig. 2).

Similar patterns were shown when we modeled heavy fishing in the first 5 years (F=2.0), and uniform low mortality was evident thereafter. Curves of biomass on age showed a much larger decrease in biomass with increasing M and F (Fig. 3; Table 4). Maximum biomass at minimum fishing mortality (F=0.02; M=0.02–0.12) was 81–67% less than seen without heavy early mortality. For example, under the most likely combinations of M and F_{CUR} for the Chesapeake Bay fishery, biomass was reduced approximately 82–87% (M=0.06 F_{CUR}=0.06; M=0.08 F_{CUR}=0.04).

Values of $t_{CRITCAL}$ estimated by using different values of M were relatively high for black drum in Chesapeake Bay. Increasing M resulted in a decrease in $t_{CRITICAL}$ from 25 yr at M=0.02 to 10 yr at M=0.12. This finding indicates that, for the range of M considered in our study, maximum theoretical cohort biomass, in the absence of fishing, is achieved before black drum reach age 25. This occurs at the lowest value of M, approximately the mean age of capture in Chesapeake Bay. For the most likely combinations of M and F (M=0.06 F_{CUR}=0.06; M=0.08 F_{CUR}=0.04), $t_{CRITICAL}$ declined from 13(M=0.08)–15(M=0.06) yr in the unfished stock to 10 yr in the fished stock. In this example, $t_{CRITICAL}$ is below the mean age of capture in the Bay, 26 yr, and potential yield is lost to natural mortality.

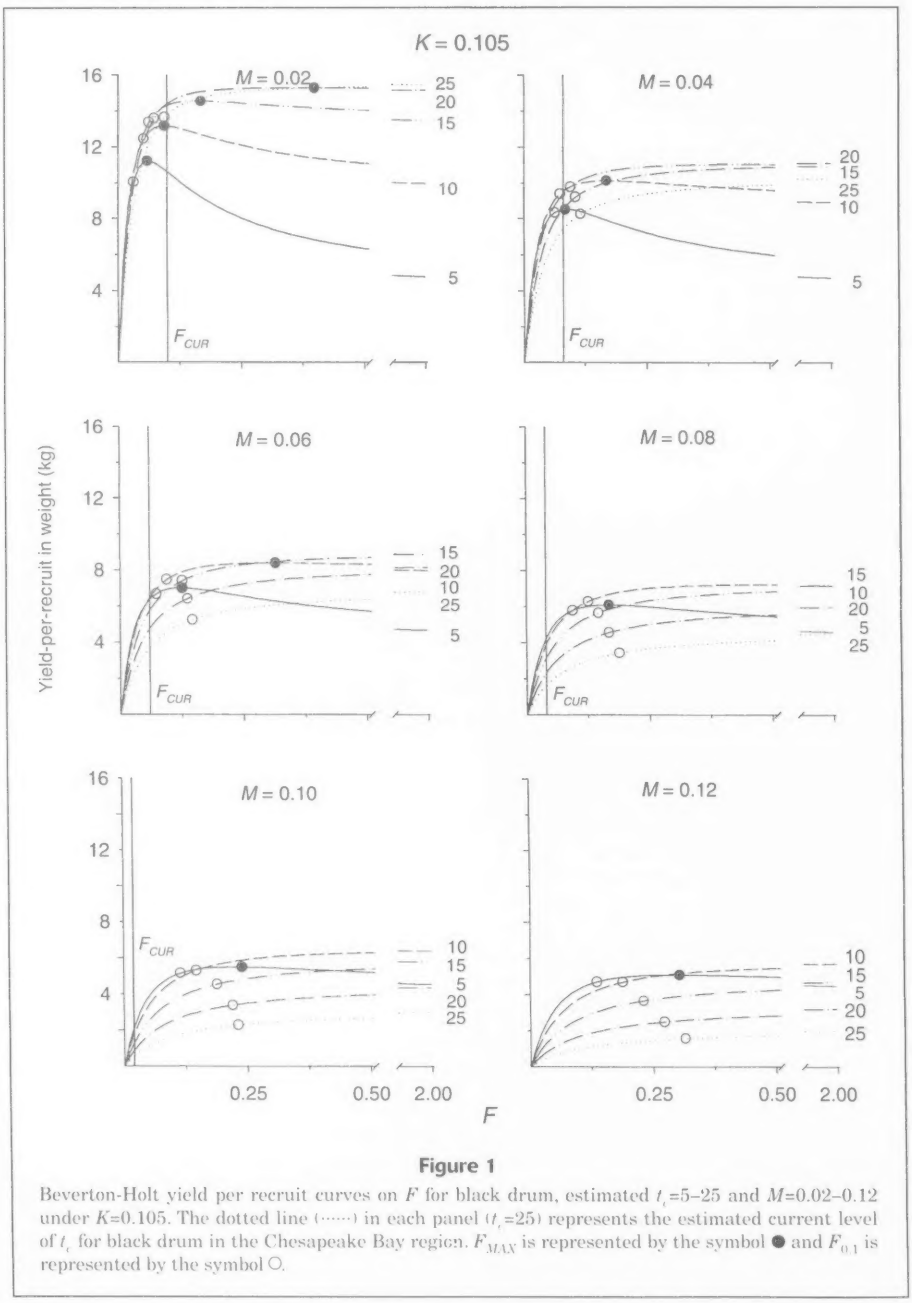

Figure 1

Beverton-Holt yield per recruit curves on F for black drum, estimated t_c=5–25 and M=0.02–0.12 under K=0.105. The dotted line (·····) in each panel (t_c=25) represents the estimated current level of t_c for black drum in the Chesapeake Bay region. F_{MAX} is represented by the symbol ● and $F_{0.1}$ is represented by the symbol ○.

Estimated values of $P_{\bar{E}}$ were also low for black drum caught in Chesapeake Bay. For L_∞=117 cm, and the current estimated l_c (110 cm, corresponding to t_c=25), $P_{\bar{E}}$=0.06, i.e. on average, only 6% of their potential growth still remains when black drum in Chesapeake Bay enter the exploited phase at age 25. For alternative values of t_c equal to 5, 10, 15, 20, and 30 years, values of $P_{\bar{E}}$ are 0.46, 0.27, 0.16, 0.09, and 0.03, respectively.

Modeling with K=0.124

Yield modeling was also done to encompass an alternative estimate of growth based on the Brody coefficient (K) determined from the northeast Florida fishery (Murphy and Taylor, 1989). Because Chesapeake Bay region catches did not include fish aged 1–5, the estimate of K (0.105; Jones and Wells, 1998) differed slightly from that esti-

Table 2

Estimates of $F_{0.1}$ and F_{MAX} compared to F_{CUR} from Beverton-Holt yield-per-recruit modeling for various levels of K, M, and t_c. The symbol *** indicates that F_{MAX} occurs at the highest values of F. $F_{CUR(i)}$ was calculated from the upper-bound estimate of Z (as $F_{CUR(i)}=Z-M_i$) and represents the upper-bound estimate of current F.

K	M	t_c	$F_{0.1}$	F_{MAX}	F_{CUR}	K	M	t_c	$F_{0.1}$	F_{MAX}	F_{CUR}
0.105	0.02	5	0.03	0.06	0.10	0.124	0.02	5	0.05	0.07	0.10
		10	0.05	0.09				10	0.06	0.11	
		15	0.06	0.17				15	0.07	0.23	
		20	0.07	0.40				20	0.08	***	
		25	0.09	***				25	0.09	***	
	0.04	5	0.06	0.08	0.08		0.04	5	0.06	0.10	0.08
		10	0.07	0.17				10	0.07	0.24	
		15	0.09	0.51				15	0.09	1.38	
		20	0.10	***				20	0.12	***	
		25	0.12	***				25	0.12	***	
	0.06	5	0.07	0.13	0.06		0.06	5	0.08	0.15	0.06
		10	0.09	0.31				10	0.10	0.47	
		15	0.11	***				15	0.13	***	
		20	0.13	***				20	0.14	***	
		25	0.15	***				25	0.14	***	
	0.08	5	0.09	0.17	0.04		0.08	5	0.09	0.21	0.04
		10	0.12	0.61				10	0.14	1.11	
		15	0.15	***				15	0.17	***	
		20	0.17	***				20	0.19	***	
		25	0.19	***				25	0.20	***	
	0.10	5	0.11	0.23	0.02		0.10	5	0.12	0.28	0.02
		10	0.15	1.51				10	0.18	***	
		15	0.19	***				15	0.20	***	
		20	0.22	***				20	0.23	***	
		25	0.25	***				25	0.27	***	
	0.12	5	0.13	0.30	0.00		0.12	5	0.14	0.39	0.00
		10	0.19	***				10	0.20	***	
		15	0.23	***				15	0.25	***	
		20	0.27	***				20	0.29	***	
		25	0.311	***				25	0.30	***	

Table 3

Lifetime cohort biomass (g) from the Ricker biomass model (Saila et al. 1988) under M=0.02–0.12, and uniform F=0–0.12. Integration was by rectangular approximation. Simulations were based on an arbitrary starting biomass of 1000 g.

	F						
M	0	0.02	0.04	0.06	0.08	0.1	0.12
0.02	180,730	107,915	70,195	49,170	36,595	28,595	23,210
0.04	107,915	70,195	49,170	36,595	28,595	23,210	19,420
0.06	70,195	49,170	36,595	28,595	23,210	19,420	16,675
0.08	49,170	36,595	28,595	23,210	19,420	16,675	14,600
0.10	36,595	28,595	23,210	19,420	16,675	14,600	13,040
0.12	28,595	23,210	19,420	16,675	14,600	13,040	11,750

mated for northeast Florida (K=0.124) which did include these ages. The values for L_∞ were virtually identical from both studies Model results based on this faster growth rate produced similarly shaped yield-per-recruit curves but with slightly higher yields and benchmark values (Fig. 4). At the most probable values of M (0.06; 0.08), yield-per-recruit curves peaked only at $t_c \leq 10$ yr. Otherwise, curves were asymptotic or rising. F_{MAX} at t_c=5 yr was 0.15 for

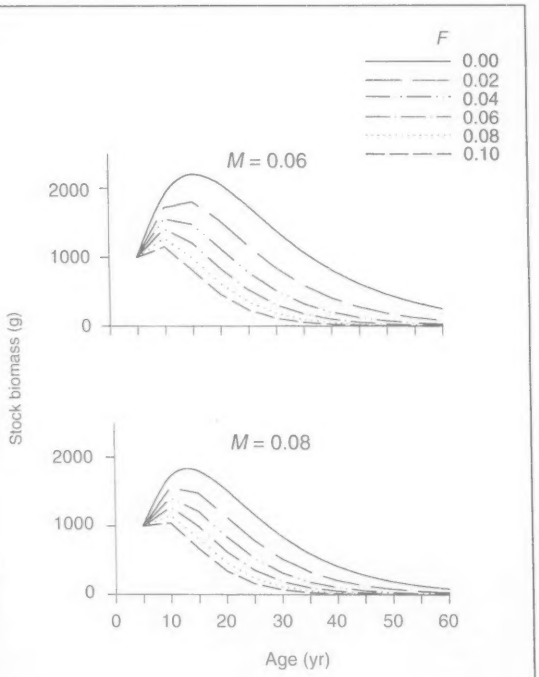

Figure 2

Ricker biomass curves under conditions of low, uniform instantaneous fishing mortality, F=0.0–0.1 and M=0.06–0.10. The dash-dot-dot-dash (—··—) and dash-dot-dash (—·—) lines represent the most likely range of current fishing mortality, F_{CUR}=0.04 and 0.06, respectively. Note that recruit biomass is arbitrarily set at 1000 g.

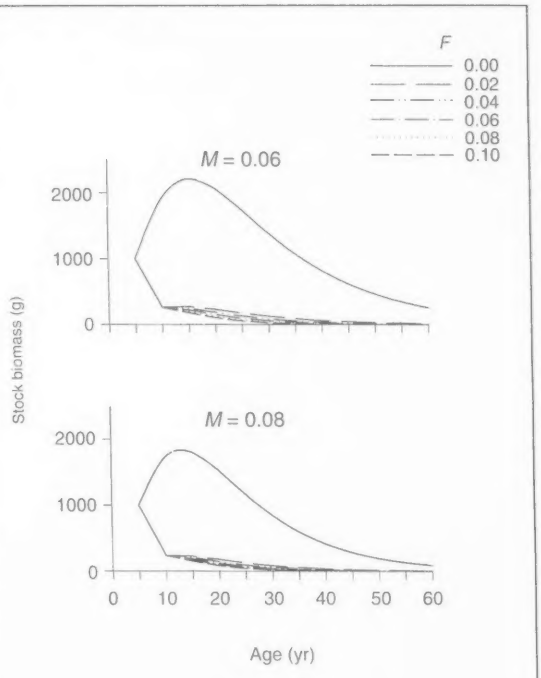

Figure 3

Ricker biomass curves under conditions of high instantaneous fishing mortality, F=2.0, in the first 5 years with low, uniform F=0.0–0.1 thereafter and M=0.06–0.10. The dash-dot-dot-dash (—··—) and dash-dot-dash (—·—) lines represent the most likely range of current fishing mortality, F_{CUR}=0.04 and 0.06, respectively. Note that recruit biomass is arbitrarily set at 1000 g.

Table 4

Lifetime cohort biomass (g) from the Ricker biomass model (Saila et al. 1988) under M=0.02–0.12, and F=2.0 over the first 5 years and low uniform F=0–0.12 thereafter. Integration was by rectangular approximation. Simulations were based on an arbitrary starting biomass of 1000 g.

	F						
M	0	0.02	0.04	0.06	0.08	0.1	0.12
0.02	180,730	20,395	15,785	13,075	11,390	10,270	9495
0.04	107,915	14,750	12,305	10,775	9760	9055	8560
0.06	70,195	11,610	10,225	9315	8675	8225	7875
0.08	49,170	9730	8895	8325	7910	7600	7370
0.10	36,595	8525	8000	7630	7360	7145	6990
0.12	28,595	7730	7380	7130	6940	6785	6660

M=0.06 and 0.21 for M=0.08 (Table 2), greater than our estimate of Z and F_{CUR}. At t_c>10, F_{MAX} occurred at the highest levels of F. At the most probable levels of M, $F_{0.1}$ was greater than F_{CUR} (Table 2). Hence under either F_{MAX} or $F_{0.1}$ and larger K, F_{CUR} was still below that needed to obtain maximum yields from the fishery in Chesapeake Bay.

Similarly, model results from this faster growth (K=0.124) and broader levels of M (0.02–0.12) showed that F_{CUR} is below F_{MAX} and $F_{0.1}$ for Bay region fisheries except

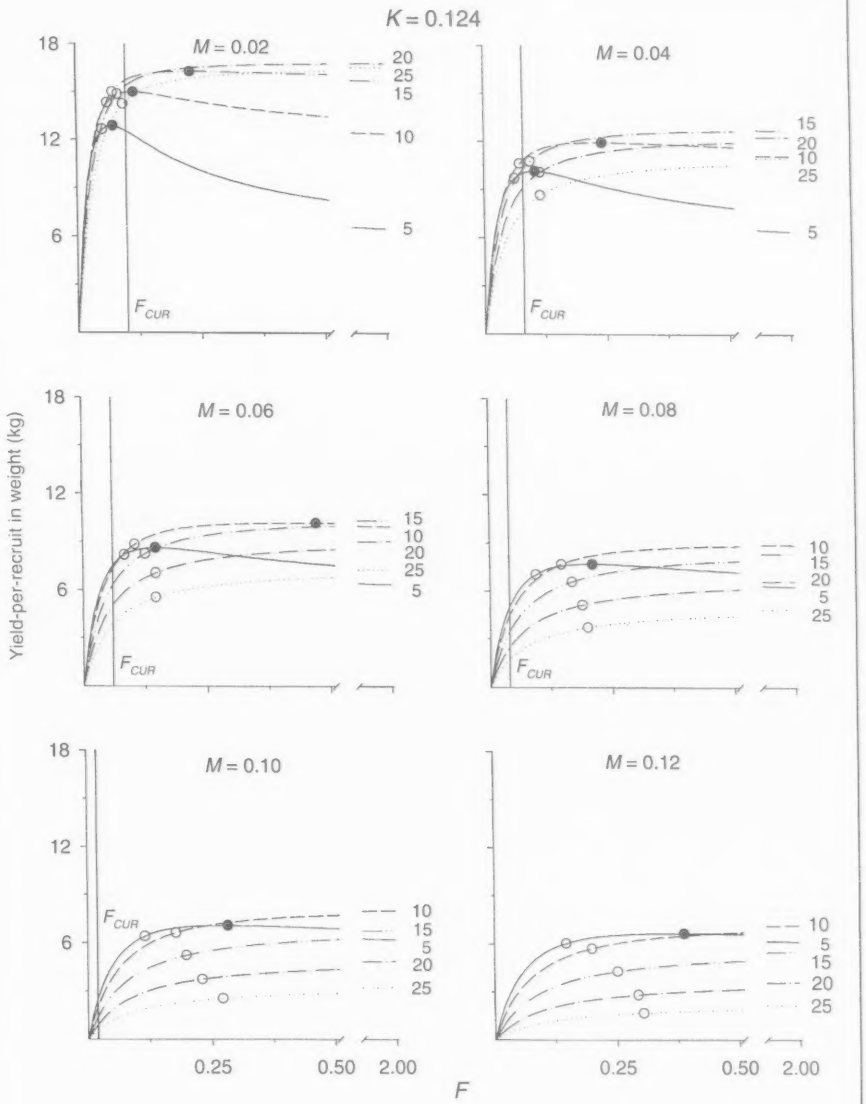

Figure 4

Beverton-Holt yield per recruit curves on F for black drum, estimated t_c=5–25 and M=0.02–0.12 under K=0.124. The dotted line (·····) in each panel (t_c=25) represents the estimated current level of t_c for black drum in the Chesapeake Bay region. F_{MAX} is represented by the symbol ● and $F_{0.1}$ is represented by the symbol ○.

for $M \leq 0.04$. Yield values were slightly higher than for K=0.105 for all levels of M (Fig. 4; Table 2), and the benchmarks, F_{MAX} and $F_{0.1}$, fell at higher values of F. Hence, the reasoning that was used to discount growth overfishing previously can also be used here. When M=0.02–0.04, yield-per-recruit curves peaked at t_c =5–15 yr and were asymptotic or rising at older ages. Both scenarios indicated that growth overfishing is possible but improbable because of the unlikely maximum ages that such low values of M imply and because curves peaked at values of t_c lower than those experienced in this fishery. At higher levels of M (0.10; 0.12), growth overfishing was even less likely than at slower growth levels. Yield-per-recruit curves peaked only at t_c=5 and for F>0.28. Likewise, this t_c was too young for the fishery, and Z and F_{CUR} were considerably smaller than the lowest values of F_{MAX} or $F_{0.1}$. Hence,

even when the full range of M and faster growth were considered, growth overfishing was not likely for the Chesapeake Bay region fishery.

Overall, yield-per-recruit curves showed that a sixfold increase in M resulted in a 50% decrease in yield for both growth rates (Figs. 1 and 4). As M increased, yield-per-recruit decreased. For a given M, yield-per-recruit increased to a maximum at an intermediate level of t_c. Increases in yield slowed from 5–15 yr and decreased from maxima thereafter at older ages. In only one case (M=0.02 and K=0.105), yield-per-recruit increased with increased t_c up to 20 yr. In all other cases, yield decreased for t_c>20 yr, indicating that, beyond 20 yr, biomass was lost to natural mortality.

Discussion

Our results indicate that yield-per-recruit for black drum in the Chesapeake Bay region is below its maximum for all but the lowest values of M used in our simulations. For $M \geq 0.04$, current fishing mortality was below F_{MAX}. Only when M=0.02 and t_c<15 does the upper bound of F_{CUR} fall above F_{MAX} . We discounted this case of extreme low M because of the unusually long lifetime that it predicts—some 200 years. Yield-per-recruit and economic efficiency could be maximized for black drum in Chesapeake Bay by decreasing t_c to 5 years along with higher rates of fishing mortality. However, this may not be the most viable management option for this species for several reasons. First, because the relation between yield-per-recruit and F is essentially asymptotic, harvesting black drum in the Bay at or near F_{MAX} would require a huge increase in fishing effort, making harvest of this species economically inefficient, especially with the current low demand for these fish. Besides, benchmarks such as F_{MAX} are no longer thought to provide a sustainable measure of long-term maximum yield from a fishery. Second, the current t_c may reflect the mean age of migrating adults that are recruited to the fishery. If so, decreasing t_c may not be possible because young fish may not undertake migration along the coast, and a decrease in mesh size may result in failure of the net to "gill" the larger fish, with the result that catches would be diminished.

Large reductions in biomass, especially of older fish, were shown in biomass modeling. Biomass decreases 42–59% under the most likely values of mortality (M=0.08, F_{CUR}=0.04; M=0.06, F_{CUR}=0.06, respectively) more than that of the unfished stock. Reductions in biomass (up to 87%) are exacerbated when heavy fishing mortality is concentrated on young fish. Concurrent with these reductions in biomass, is a rapid and dramatic loss of older fish from the stock. This juvenescence occurs quickly—$t_{CRITICAL}$ is reduced from 15 in the unexploited stock to 10 at F=0.02 for M=0.06, and from 13 to 10 at M=0.08. At greater F, the decrease in $t_{CRITICAL}$ is even greater and the abundance of older fish diminishes further.

Altogether these modeling results show no indication of growth overfishing in the Chesapeake Bay region where old fish are predominantly targeted. Moreover, it is difficult to growth overfish a stock when fishing concentrates on capturing primarily older, larger fish. For example, black drum have already obtained 58% of their lifetime growth in length, and 22% of their lifetime weight when they first recruit to the Chesapeake Bay region at age six (Jones and Wells, 1998). By their mean age of capture in this region, they have obtained 90% of their lifetime growth in length and 51% in weight. Exploited cohorts have already surpassed their maximum growth by the time they enter the Bay region, and thereafter, natural mortality predominates. Cohort biomass has already declined from its optimum by the age fish enter the exploited stock in the Bay region.

Although these modeling results show no indication of growth overfishing in Chesapeake Bay, they do indicate that black drum are vulnerable when heavy fishing is directed to young fish in the southern portion of their range along the U.S. East Coast. We chose a high level of F in the first five years of life to dramatically illustrate the effect of targeted fishing on small fish and the potential effects of bycatch from other fisheries. These simulations clearly indicate the importance of limiting fishing mortality in regions where young fish occur. Prior to 1989, black drum landed in the Florida east coast commercial fisheries averaged 320 mm (Murphy and Muller[2]), and 80% of the catch was 4 yr or younger (Murphy and Taylor, 1989), raising the potential of growth overfishing at that time. Capture at this young age also raises concern for recruitment overfishing, which our modeling does not address, especially when fish are targeted before they can reach sexual maturity (age 5). The potential for recruitment overfishing is minimal in areas, such as Chesapeake Bay, where the fishery targets older fish that have reproduced for many years before capture. Moreover, recent bans on gillnetting in Florida and other regulations on black drum fishing since 1989 should preclude recruitment overfishing and help preserve the stock.

Models are typically used in management to regulate fishing mortality in order to obtain sustainable harvests from a stock. These regulations have historically resulted in harvests with large biomass that are valued in commercial fisheries. In contrast, recreational anglers are not as interested in obtaining maximum biomass as they are in catching fewer, but larger fish. Moreover, increased production of larger fish occurs when fishing mortality is below F_{MAX} and when recruitment is high. Hence, in the black drum fishery, which is targeted by both commercial and recreational fishermen, management objectives are at cross purposes. The commercial fishery benefits when yields are maximized to the detriment of survival and growth for the trophy-size fish desired by recreational anglers. In the Chesapeake Bay region, fishing mortality is low and supports the objectives of managing the recreational fishery. However, the most influential fishing mortality is on young fish and is not under the control of the Bay region management agencies, but is controlled by states farther south.

The long-range migrations of the East Coast black drum stock argue for a coast-wide management strategy. Through our modeling, we have shown that fishing practices in the Bay region have little impact on the production

of harvestable biomass and that mortality on young fish drives eventual production available to the Chesapeake Bay region black drum fishery. The supply of fish to the Bay region depends on mortality during the first ten years of life, years when these fish are found off the coasts of the South Atlantic states. Hence, management practices by states south of Cape Hatteras will determine the supply of fish to this coast-wide stock.

Acknowledgments

We would like to thank Barbara McClellan for her assistance with modeling and graphics, and Douglas Vaughan and Michael Murphy for their review of and suggestions for improving this manuscript. This research was funded by a Wallop/Breaux Program Grant for Sport Fish Restoration from the U.S. Fish and Wildlife Service through the Virginia Marine Resource Commission, Project F-88-R3 to C. Jones and Mark E. Chittenden Jr.

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Abstract–A learning curve analysis is applied to model the change in effort units with time by the commercial fishery for Atlantic cod (*Gadus morhua*) in the Barents Sea. The results indicate that fishing efficiency has increased and that the adjusted commercial catch per unit of effort (CPUE) is more strongly related with stock abundance.

Adjustment of commercial trawling effort for Atlantic cod, *Gadus morhua*, due to increasing catching efficiency

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Fishing fleets and individual fishing vessels are expected to increase their efficiency with time owing to technological improvements. This is a serious problem when a time series of commercial catch per unit effort (CPUE) is used to measure trends in fish stock abundance (Gulland, 1983). A standard effort unit will gradually remove a greater proportion of the stock, and the CPUE corresponding to a given fish stock abundance will increase. Commercial effort units should, therefore, be adjusted to account for gradual changes in catchability (Gulland, 1983).

A learning curve describes how unit costs decline as organizations gain experience in production (Argot and Epple, 1990). The general form of the learning curve is given by

$$y = ax^{-b}, \quad (1)$$

where y = the number of direct labor hours required to produce the xth unit;
a = the number of labor hours required to produce the first unit;
x = the cumulative number of units produced; and
b = the parameter measuring the rate at which labor hours are reduced as cumulative output increases (Argot and Epple, 1990).

If a learning curve is used to describe a fishery, the labor hours required to produce the xth unit can be translated into the effort required to catch a certain fraction of the fish stock, termed effort per stock fraction (*epsf*). Time, instead of cumulative catch, is assumed to be a better measure of x because fishermen learn even if stock abundance and catches are low. In this study, appropriate learning curves are fitted to the decrease in *epsf* with time for vessels in the Norwegian bottom trawler fleet in the fishery for Atlantic cod (*Gadus morhua*). Effort is then adjusted by using the fitted learning curve, to generate CPUE-indices that better reflect fish stock abundance.

Materials and methods

To calculate the effort per stock fraction (*epsf*) for a given vessel, effort is divided by the ratio of catch and fishable stock biomass (stock fraction caught) in a given time period:

$$epsf = \frac{e}{\left(\frac{c}{B_f}\right)} = \frac{B_f \cdot e}{c}, \quad (2)$$

where B_f = the estimated weight of fishable biomass; and
e = the total effort and c is the total catch (weight) during the time period.

The catch and effort data should be independent from the estimate of B_f. Some catch composition criteria should also be introduced to increase the probability that the vessels were part of the targeted fishery during the period. Note that *epsf* is the inverse of catchability.

By inserting *epsf* for y and time (t) for x in Equation 1, then

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$$\ln(epsf) = \ln(a) - b \cdot \ln(t). \quad (3)$$

By fitting a regression line to $\ln(epsf)$ versus $\ln(t)$, estimates of the parameters $\ln(a)$ and b in the learning curve are obtained. An unbiased estimator for a is $\exp(\ln(\hat{a})+ MSE/2)$ (Casella and Berger, 1990), where $\ln(\hat{a})$ is the intercept of the regression line and MSE is the mean squared error from the regression. A learning curve can be estimated at the fleet level by using average *epsf* of the vessels, and at the vessel level by using an individual vessel's *epsf*. These two approaches are somewhat different because the efficiency of a fleet is increased both by improvement of existing vessels and by addition of new and better vessels.

The effort units in a time series of CPUE can be adjusted to the level of one of the elements (index time) in the time series as follows:

$$e_i^* = e_i \left(\frac{epsf_{index}}{epsf_i} \right), \quad (4)$$

where e_i^* = the adjusted effort at time i; and
$epsf_{index}$ and $epsf_i$ = the effort per stock fraction modelled with the estimated learning curve at the index time and time i, respectively.

Note that the learning curve model is a continous function and CPUE is normally given as a discrete time series. Time i should, therefore, correspond to the midpoint of the time interval over which the corresponding CPUE observation is calculated.

The catch and effort data were taken from a logbook database collected by the Norwegian Directorate of Fisheries. Logbooks from the Norwegian bottom trawler fleet have been recorded since 1971 and each individual record includes vessel, species, date, and summarized duration (in hours) and summarized catch (in kilograms) of the trawl hauls each day. Estimates of trawlable biomass (B_t) of Atlantic cod in the Barents Sea were taken from VPA (virtual population analysis) estimates of stock biomass at the beginning of each year (ICES[1]). Only 20% of the 3-year-old cod and 50% of the 4-year-old cod were considered to belong in the trawlable part of the biomass because of mesh selection in the trawls. This selection of young cod corresponded broadly to the retention probabilities in the beginning of the year based on a trawl selection curve. The effort (e) is hours of trawling. Because the VPA estimates of stock size are given for the start of the year, the summation of catch and effort for a given year (t) are over the period from July in year $t-1$ to June in year t. In this way the stock estimates from VPA are given for the middle of the time period. Only records with more than 20% (in weight) cod for a recorded day were used to increase the probability that cod was the target species. Varying the minimum accepted proportion of a species in catches has been shown to significantly affect estimates of CPUE (Ketchen, 1964). To avoid vessels that did not take active part in the cod fishery, only vessels with at least 10 observations where more than 50% cod were present in a given year were used in the calculation of the fleet's average *epsf*. Only cod records from north of 67°N were used because this latitude is the limit of the distributional area for Atlantic cod along the Norwegian coast.

Changes in yearly *epsf* were analyzed and estimates of the parameters in the learning curve were made at the vessel level and at the fleet level (average *epsf*) in the period 1971–99. Only one vessel was active during the whole period without being rebuilt, and this vessel was chosen for analysis at the vessel level.

The trawl fishery for Atlantic cod in the Barents Sea has existed since about 1920, but the Norwegian trawler fleet did not significantly participate in this fishery until after the end of the Second World War. Year one in the learning process for the Norwegian trawler fleet is therefore set at 1946. In the present study, sufficient data for estimating learning curves exist only from 1971, which is a limited part of the time period in which the Norwegian fishery has existed. This causes the year 1972, the first year where it is possible to estimate *epsf*, to become year 27 in the learning process.

A time series of CPUE for Atlantic cod of the Barents Sea was calculated by using the same catch and effort data as above, and yearly effort was adjusted (Eq. 4) to the level of 1972 by using the estimated learning curve on the fleet level. Only records containing more than 20% cod (in weight) were used. CPUE was set as total catch divided by total effort in the period from July in year $t-1$ to June in year t.

Results

The estimates of annual *epsf* showed a decreasing trend with time both at the fleet level and at the vessel level (Fig. 1, A and C). The slope and intercept of the fitted regression line at the fleet level (Fig. 1B) were 1.742 and 14.272, respectively, and the correlation given as the r^2-value was 0.50. At the vessel level the values of the slope and intercept (Fig. 1D) were 1.538 and 13.334, respectively and r^2 was 0.55. The estimated a was 1895039.044 at the fleet level and 714722.761 at the vessel level. The slopes of the two regression lines were significantly different from zero ($P<0.0001$), but the two regression lines were not significantly different from each other ($P>0.05$).

The time series of annual CPUE became much more similar to the biomass estimate from VPA when effort was adjusted (Fig. 2), especially in the first and last part of the time period. In the middle of the period (after 1980) the trend in adjusted CPUE suddenly became different from that of biomass estimates from VPA, and CPUE values were much higher than biomass in relation to the ratio in the first and last part of the period for some years.

[1] ICES (International Council for the Exploration of the Sea). 2000. Report of the Arctic Fisheries Working Group, Copenhagen, 23. August–1. September 1999. ICES CM 2000/Assess:3, 311 p. ICES, Palægade 2-4 DK-1261 Copenhagen K, Denmark.

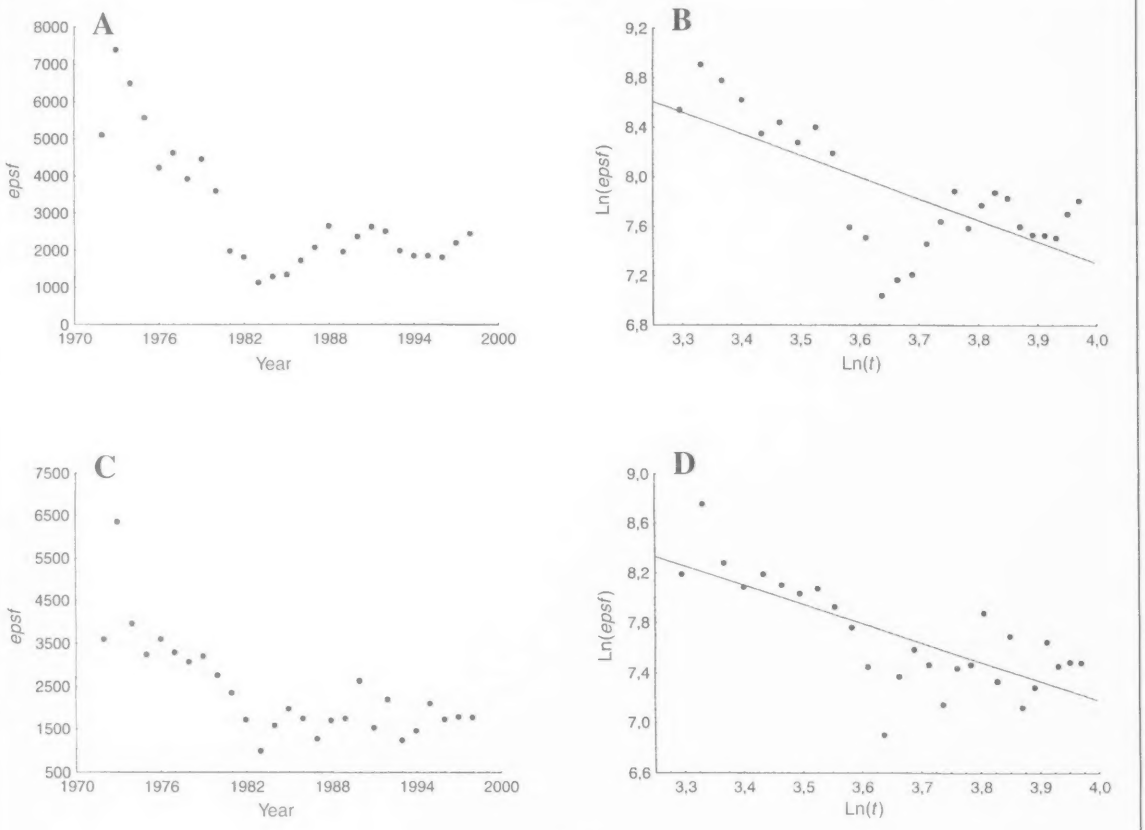

Figure 1

Relation between average effort per stock fraction (*epsf*) per vessel in the fleet and year (**A**), *epsf* for an individual vessel and year (**C**), log-transformed *epfs* and time (in ln(years)) for the average vessel in the fleet (**B**) and for an individual vessel (**D**). Note that the first observed time value in B and D is ln(27) because 1946 is assumed to be the first year in the learning process. The slope and intercept for the fitted lines and the correlation between the variables in B and D are given in the text.

Discussion

A learning curve ideally requires data points from the initial phase of the process. For many fish stocks, catch and effort data, together with an independent estimate of total biomass, exist only for recent years. Given the approximate year the fleet entered the fishery, it is necessary to assume that *epsf* follows the learning curve pattern from that year onwards. Under this assumption, it is possible to adjust effort backwards in time to the level of one year in the time series by using the estimated learning curve. Technical revolutions, such as the introduction of hydraulic wires, may cause a very dramatic change in the fishery, and if this happens the learning curve should be estimated from the time when the new technology appeared. Good knowledge about the history of the fishery is thus necessary. There are also alternative methods for dealing with increases in efficiency with time in a fishery. Gulland (1983) suggested constant monitoring of the changes in the fishing gears by conducting experiments. This solution may, however, be very expensive.

The question whether the effort should be adjusted with a learning curve from the fleet level or from the vessel level depends on the resolution of the catch and effort data and on other standardization of effort. If effort is first adjusted within the fleet because of the individual differences in fishing power, adjustment of the effort due to learning should be based on a learning curve from the standard vessel or the group of standard vessels to avoid double standardization. It is important to be aware that individual vessels also may show different learning rates and these may differ from the average learning rate of the fleet. An individual vessel may improve its efficiency by increasing the cooperation with other vessels, by buying better searching equipment and more efficient fishing gear, and by hiring more skilled crew.

An important assumption in this work is that a constant fraction of the stock is caught when the fleet has a constant efficiency. Many fish stocks, including the Atlantic cod stock in the Barents Sea, have a seasonal cycle in availability to the fishing fleet because of regular spawning and feeding migrations that cause large peaks in the density of fish. The assumption above is therefore violated if the spatial and temporal distribution of effort in the fleet during the year changes between years. Correction for changes in the seasonal distribution of effort between years are, however, described by e.g. Gulland (1983) and Gavaris (1980). Around 1979 quotas and fishery regulations were introduced in the Norwegian fisheries. As seen from the outliers in Figure 1, it is obvious that something affected the *epsf* after 1980. Dramatic responses are expected when a fishery is regulated (Hilborn and Walters, 1992). Respones to regulations may include changes in the effort distribution during the year, changes in the patterns of competition and cooperation with other vessels, increased misreporting, and increased amounts of discards.

In addition to uncertainties in the reported catch and effort from the vessels, there are also uncertainties in the VPA estimates of stock size (see Ulltang, 1977). The trawlable fraction of the youngest year classes also changes within and among years due to individual growth and yearly differences in growth. The constant retention probabilities used in this work to select the youngest age classes from the VPA estimates, and the use of only one single stock estimate per year is thus, perhaps, an over simplification. To get a better estimate of the learning curve, *epsf* can be estimated based on averaging effort and catch over shorter time periods than in this work. This requires, however, advanced modelling of the selection process, and possibilities for obtaining estimates of total abundance more than once a year.

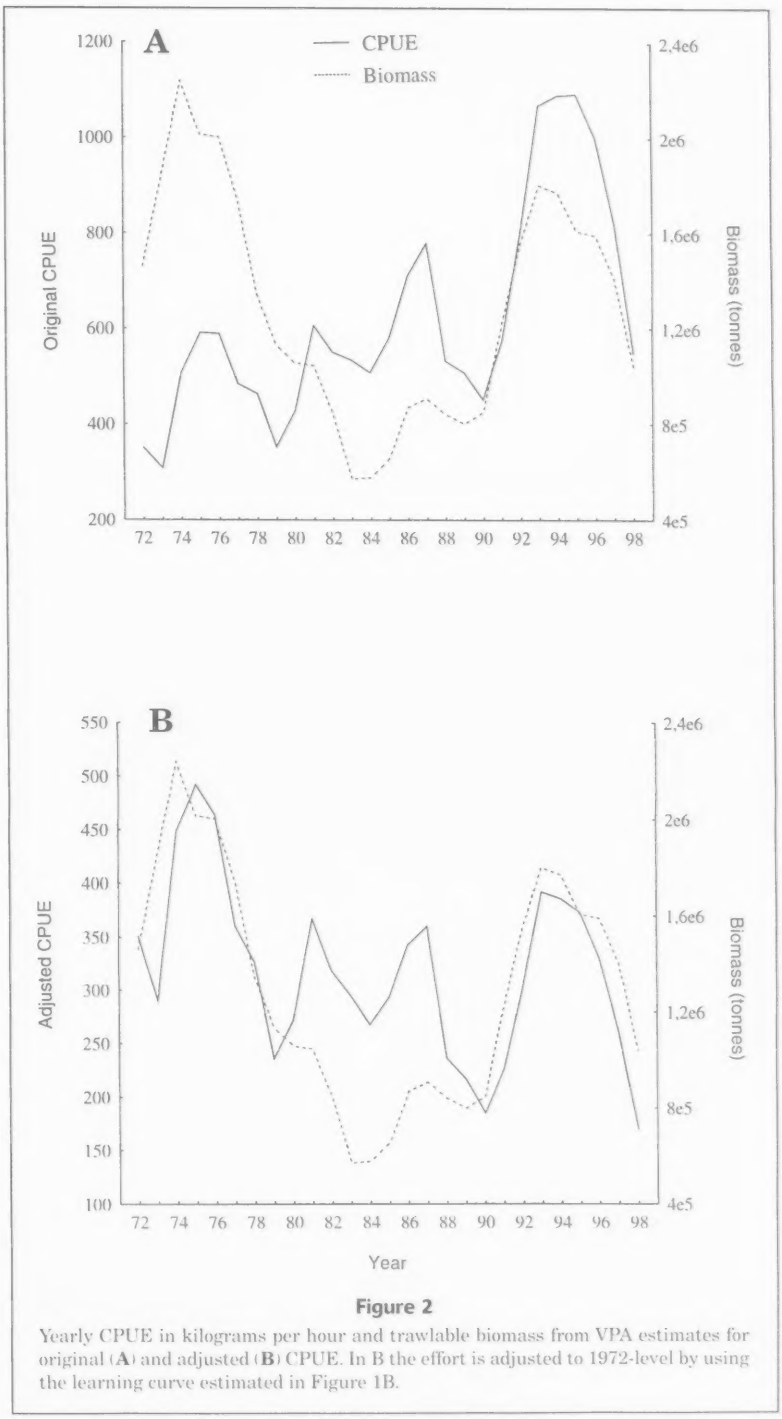

Figure 2

Yearly CPUE in kilograms per hour and trawlable biomass from VPA estimates for original (**A**) and adjusted (**B**) CPUE. In B the effort is adjusted to 1972-level by using the learning curve estimated in Figure 1B.

The VPA estimates and the catch and effort data used in this work are not totally independent from each other. A time series of commercial CPUE from the Norwegian trawler fleet was used, together with other CPUE time series, to calibrate the most recent VPA estimates of the old-

est fish (owing to lack of survey data for old fish). Total catch data from the fleet were also used in the VPA procedure. Converged VPA were, however, fairly independent of CPUE, and the limited dependence was not considered to have a large effect on the learning curve estimation.

It seems reasonable, as seen from the plots in Figure 1, to assume that *epsf* followed a learning curve pattern with time. The outliers around 1980 affected the regression lines in Figure 1 (B and D) considerably. If these outliers were caused by the fishermens' response to the new regulations, they should perhaps be removed. Another solution is to develop learning curve models that account for such strong interventions.

The sudden change in the relation between CPUE and VPA estimates in Figure 2 may have been caused by the introduction of fishery regulations, but there are other important factors affecting the use of CPUE as an index of abundance. Some of these factors are similar to those mentioned above, under the discussion of the assumptions concerning the estimation of *epsf*. Another explanation for the sudden change of the ratio between CPUE and biomass estimates from VPA in Figure 2B and for the outliers in Figure 1 around 1980 is that CPUE and *epsf* (or equivalently the catchability) are functions of stock abundance. An increase in catchability at low stock size is suggested in Figure 2 by the relatively high catch rates (given the low biomass) in the early to mid 1980s. This increase may, however, be contradicted by the similar trend in biomass and adjusted CPUE in Figure 2B at the end of the time period, when stock abundance became relatively low again. If catchability is shown to be density dependent for Atlantic cod in the Barents Sea, it should be incorporated into the model when the learning curve is fitted. Both long-term changes (e.g. Gordoa and Hightower, 1991; Swain et al., 1994) and density-dependent changes (Crecco and Overholtz, 1990; Rose and Kulka, 1999) in catchability of gadoids have been indicated when commercial CPUE is being used as an index of abundance.

Conclusion

Modeling of *epsf* using the learning curve seems be a promising method for solving the old and well-known problem of learning when time series of commercial CPUEs are used as indices of abundance. Care needs to be taken when selecting data and observations for estimation of learning curves, especially in multispecies fisheries.

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Assessment of skipjack tuna (*Katsuwonus pelamis*) spawning activity in the eastern Pacific Ocean

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Abstract—An investigation of skipjack tuna, *Katsuwonus pelamis*, spawning activity was conducted to test an earlier established and widely accepted hypothesis that significant spawning of skipjack does not occur in the eastern Pacific Ocean (EPO). Skipjack tuna ovaries were collected, from fish greater than 50 cm in length, from commercial landings of purse seiners fishing in the EPO during 1995. A total of 76 samples, each consisting of approximately 25 females, were collected, processed, and analyzed. The characteristics used to classify the reproductive condition of the individual fish were the mean diameter of the oocytes of the most advanced mode and the presence or absence of residual hydrated oocytes. Results indicate that significant spawning of skipjack tuna, 50 cm or greater in length, occurs in areas of the EPO where sea surface temperatures are equal to or greater than 24°C.

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Skipjack tuna, *Katsuwonus pelamis*, are distributed throughout the Pacific Ocean in tropical and subtropical waters, where they are a primary target species of large-scale purse-seine fisheries. Total estimated catches now exceed one million metric tons. In the eastern Pacific Ocean (EPO), skipjack tuna have been fished from 34°N, off southern California, to 27°S, off northern Chile (Collette and Nauen, 1983; Matsumoto et al., 1984; Wild and Hampton, 1994). The fishery in the EPO was historically concentrated in two areas, a southern area at about 5°N to 10°S and east of 110°W, and a northern area at about 10°N to 30°N and west of 105°W to about 125°W. Estimated annual catches of skipjack tuna during the 1988 to 1997 period in the EPO averaged about 97 thousand metric tons, ranging from 63 to 159 thousand metric tons (Table 3 in Bayliff, 1999). The catches in the southern area have generally been twice as large as those in the northern area, and there have been large annual fluctuations in both areas. Since 1995, the greatest catches have been made by purse seiners setting on floating objects, including fish-aggregating devices (FADs), between about 10°N and 15°S from the coast of the Americas to about 140°W.

Schaefer (1963), reporting on population structure of skipjack tuna in the eastern Pacific, stated that "some, at least, of the West Coast population range far to the westward." He further stated that, "most important, there is little evidence of skipjack tuna spawning in the eastern Pacific fishing region, or near to it; most reproduction occurs farther westward." Rothschild (1965), however, hypothesized that "most skipjack taken by the eastern Pacific skipjack fisheries originate in the central Pacific." His hypothesis was based on available evidence, at that time, from larval distributions, gonad indices, size distributions, tag recoveries, catch predictions, and immunogenetic studies. This hypothesis, however, regarding the origin of skipjack tuna that occur in the eastern Pacific may not be completely valid. The results of research on the reproductive biology of skipjack tuna in the EPO (Schaefer and Orange, 1956; Orange, 1961) indicated some spawning off Central America and in the vicinity of the Revillagigedo Islands, Mexico. In addition, larval surveys have indicated that skipjack tuna spawning occurs in offshore waters and, to a lesser extent, in coastal waters of the EPO (Matsumoto, 1975; Matsumoto et al., 1984; Nishikawa et al., 1985).

In order to achieve a better understanding of the stock structure of skipjack tuna in the Pacific Ocean, an investigation of the spawning potential of skipjack tuna in the EPO was undertaken. The objective of this study was to test the hypothesis that significant spawning of skipjack tuna does not occur in the EPO.

Materials and methods

Field sampling

Skipjack tuna specimens were selected by staff members of the Inter-American Tropical Tuna Commission (IATTC) from the landings of purse seiners at processing plants in Manta (Ecuador),

Ensenada and Mazatlan (Mexico), Mayaguez and San Juan (Puerto Rico), and Cumana (Venezuela). Sampling was restricted to catches from east of 150°W from January through December 1995. The sampling program was designed to select specimens greater than 50 cm in length, in order to efficiently sample sexually mature fish (Orange, 1961), if there were any.

The area sampling strata (Fig. 1) used by the IATTC for length data (Tomlinson et al., 1992) were also used for sampling skipjack tuna specimens for the present study. The sampling was designed to collect 25 recognizable ovaries from a single purse-seine set from each area and month stratum for one year. A quota was stipulated of no more than three such samples, for a total of 75 ovaries, from each area and month stratum from which skipjack tuna were caught and unloaded. A total of 76 samples (including 11 replicates), each consisting of approximately 25 female skipjack tuna, for a total of 1822 ovaries, were collected and processed. Skipjack tuna specimens were not available for sampling from various area and month stratum during this sampling period because of the distribution of fishing effort.

Each fish was measured to the nearest centimeter with calipers. The gonads were removed, sex was determined, and the ovaries placed in a plastic bag with identification labels and frozen. The capture locations, dates, set specifications, and sea surface temperatures (SSTs) were obtained from records of scientific observers or abstracts of the vessel logbooks made by IATTC employees, or from both.

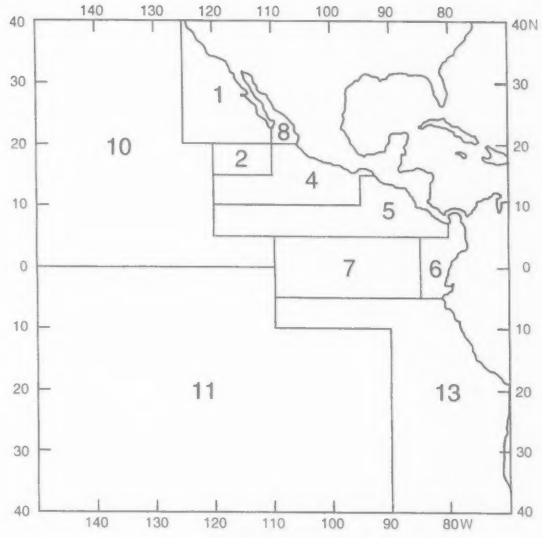

Figure 1

Areas of the eastern Pacific used for sampling skipjack tuna gonads.

Analysis of ovaries

Chi-square contingency tests were employed to compare distributions of oocyte diameters from tissue samples from the rostral, medial, and caudal regions of both ovaries from 30 fish. Because no significant differences were found ($P>0.5$), oocytes from an approximately 1-g tissue sample from the medial region of the right or left ovary were measured to the nearest 0.03 mm at 27× magnification with an ocular micrometer in a dissecting microscope. The mean diameter (random axis) was determined from 10 oocytes per fish (with oocytes >0.21 mm) present in the most advanced mode of oocytes. Ovaries were slit longitudinally and the ovarian lumen examined microscopically for the presence of residual hydrated oocytes, indicative of recent spawning activity.

Female skipjack tunas can be classified as immature, maturing, reproductively active, or resting. Skipjack have asynchronous oocyte development and are considered to be multiple or batch spawners (Schaefer, 1998; Schaefer, in press). Histological and morphological descriptions of oogenesis in the ovary of skipjack tuna (Cayré and Farrugio, 1986; Goldberg and Au, 1986; Stéquert and Ramcharrun, 1996) were used for classification of reproductive condition of individuals in the present study. The characteristics used to classify the reproductive condition of the individual fish were 1) the mean diameter of the oocytes of the most advanced mode and 2) the presence or absence of residual hydrated oocytes. A fish is classified as immature if the mean diameter of the most advanced group of oocytes is less than or equal to 0.2 mm and if there are no residual hydrated oocytes present.

Results

Sex ratios

There were 65 purse-seine sets on schools of skipjack tuna in which a minimum of 24 fish and a maximum of 87 fish, equal to or greater than 50 cm in length, were sampled (mean=52.5 cm, SE=1.44 cm). The percentage of males in the samples ranged from 26.5 to 71.3 (mean=51.5, SE=1.21). A total of 3284 fish, of which 1737 (52.9%) were males and 1547 (47.1%) were females, were sampled. The overall sex ratio for the pooled data from the 65 samples was significantly different ($\chi^2_{0.05,1}=10.99$) from the expected 1:1 ratio. Chi-square tests of males and females grouped into 5-cm length classes for the pooled data (Table 1) indicated a significant deviation in the 50–54.9 cm class (56.0% males), and the 65–69.9 cm class (57.0% males).

Replicate samples

For the 11 replicate samples collected, chi-square tests indicated no significant differences in the proportions of reproductively active female skipjack tuna specimens among the paired replicates ($P>0.05$). Thus, the sample sizes of approximately 25 female skipjack tuna from a single purse-seine set appeared to be adequate for assessing the reproductive status of the fish from the sets sampled. The data from the replicate samples were not used in any of the subsequent analyses.

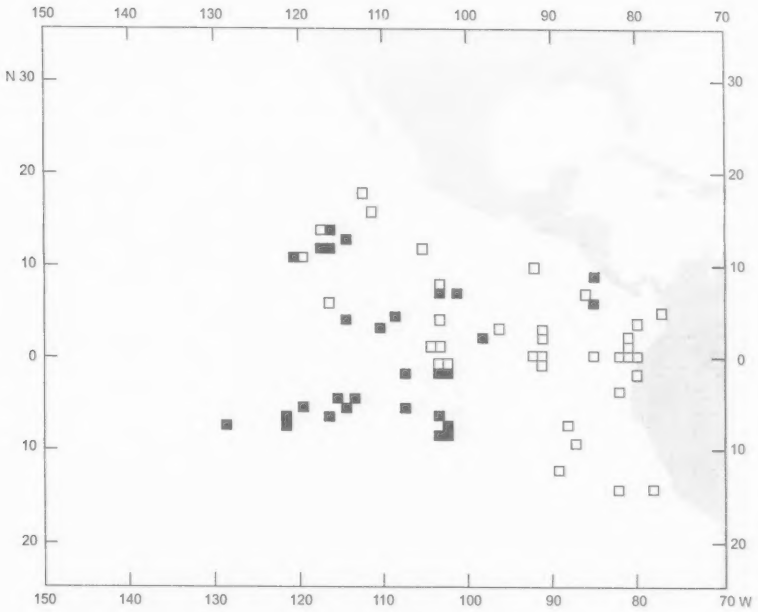

Figure 2

Distributions of reproductively-active (solid squares) and inactive (open squares) female skipjack tuna sampled during 1995.

Spatiotemporal patterns in spawning

Reproductive activity is certain for the females with advanced yolked oocytes that are equal to or greater than 0.55 mm in diameter. Of these, 429 (28%) were classified as reproductively active, and reproductively active females were found in 27 of the samples (42%) (Table 2). Of the 429 skipjack tuna with advanced yolked oocytes, 232 (54%) also had residual hydrated oocytes in the lumen of their ovaries, indicative of recent spawning. Based upon the distribution of these samples, skipjack tuna spawning in the EPO appears to be fairly widespread from around 15°N to 10°S and from the coast to about 130°W (Fig. 2). Reproductively active skipjack tuna were present north of the equator throughout the year and south of the equator during the first three quarters of the year, and there were no apparent seasonal peaks in either stratum (Fig. 3). No samples of mature fish were collected during the fourth quarter south of the equator. The length-frequency distribution of the females from the 65 independent samples is shown in Figure 4.

Based upon the SST data collected in conjunction with catch information for each of these samples, it appears that skipjack tuna are sexually inactive at SSTs less than 24°C. Of the 65 samples, 20, or 31%, were taken from skipjack tuna captured at SSTs less than or equal to 24°C (Fig. 5). In other words, just over half of the 38 samples that did not contain reproductively active fish were obtained from skipjack tuna captured at SSTs below those at which spawning occurs.

Table 1

Sex ratios of skipjack tuna, *Katsuwonus pelamis*.

Length (cm)	Number observed		Percent male	Chi-square
	Male	Female		
50.0–54.9	873	687	56.0	22.18*
55.0–59.9	365	387	48.5	0.64
60.0–64.9	252	285	46.9	2.03
65.0–69.9	226	170	57.0	7.92*
70.0–74.9	21	18	53.8	0.23
Total	1737	1547	52.9	10.99*

* = $P < 0.05$.

The frequency distributions of the estimated sizes, in metric tons, of the skipjack tuna schools sampled, along with the subset of those that were classified as spawning, are shown in Figure 6. The prominent mode in each distribution was around 25 metric tons; the ranges in each mode were from about 5 to 270 tons.

Discussion

It is evident from the results of this investigation that significant spawning of skipjack tuna, 50 cm or greater in

Table 2

Reproductive status of female skipjack tuna caught in the eastern Pacific Ocean and sampled at canneries during 1995. Area boundaries are shown in Figure 1.

	Area								
	2	4	5	6	7	10	11	13	Total
No. of samples collected	2	8	10	8	20	4	6	7	65
No. of ovaries collected	29	170	232	196	493	100	150	177	1547
No. of samples with reproductively active females	0	4	4	0	7	3	6	3	27
Percentage of samples with reproductively active females	0	50	40	0	35	75	100	43	42
No. of active females	0	44	72	0	67	55	117	74	429
Percentage of active females	0	26	31	0	14	55	78	42	28

length, occurs in areas of the EPO where the SSTs are equal to or greater than 24°C. Skipjack tuna spawning occurs throughout the year in tropical waters and seasonally in subtropical waters in all major oceans (Matsumoto et al., 1984; Nishikawa et al., 1985; Schaefer, in press). The latitudinal range in the spawning distribution of skipjack tuna has been shown for the Pacific and Atlantic Oceans to coincide with the area delineated on the north and south by the 24°C isotherm (Ueyanagi, 1969; Cayré and Farrugio, 1986). In the western part of the equatorial Indian Ocean skipjack tuna spawning also occurs throughout the year (Stéquert and Ramcharrun, 1996; Timohina and Romanov, 1996).

Earlier research on the reproductive biology of skipjack tuna in the EPO indicated spawning off Central America and off Baja California, Mexico, near the Revillagigedo Islands (Schaefer and Orange, 1956; Orange, 1961). It was concluded from these studies that skipjack tuna spawning occurs mainly offshore in the EPO, and the estimated minimum size at maturity in the vicinity of the Revillagigedo Islands is about 55 cm and about 40 cm off Central America. The present study also indicates spawning of skipjack tuna in the EPO appears to be more concentrated offshore, west of 95°W longitude (Fig. 2). It should be noted that during the 1950s and early 1960s the fishery for tunas in the eastern Pacific occurred within a few hundred miles of the mainland and in the vicinity of a few offshore islands and banks (Alverson, 1960, 1963). Thus, skipjack tuna gonad sampling for those earlier studies was confined to those areas.

Larval surveys have also indicated that skipjack tuna spawning occurs in offshore areas of the EPO and may be restricted in coastal areas (Klawe, 1963; Matsumoto, 1975; Matsumoto et al., 1984). One of the objectives of the EASTROPAC expeditions of 1967 was to look at the distribution of scombrid larvae over a vast expanse of the EPO. During EASTROPAC I (Ahlstrom, 1971), larvae of skipjack tuna (17 occurrences, 214 larvae) were collected predominantly in the offshore southern portion of the EPO at about 7°S and 120°W. Likewise, few yellowfin tuna larvae (19 occurrences, 40 larvae) were collected during EASTROPAC I, even though the spawning distribution of yellowfin tuna has been shown to be widespread throughout the EPO (Schaefer, 1998). Scombrid larvae were markedly less abundant during EASTROPAC II; few skipjack tuna (2 occurrences, 2 larvae) and yellowfin tuna (2 occurrences, 2 larvae) were collected (Ahlstrom, 1972). Catch rates of larval skipjack tuna adjusted for different size nets and different towing methods in a band of water from 10°S to 20°N indicated that skipjack tuna larval abundance was highest between 160°E and 140°W, moderate between 100°W and 140°W and between 120°E and 160°E, and low in the EPO east of 100°W (Matsumoto, 1975). The extensive compilation of data on larval scombrids by Nishikawa et al. (1985) also indicates that east of 150°W between 10°S and 10°N there is widespread spawning of skipjack tuna, mostly west of 110°W. Although there is also a distinct tendency of increasing abundance of skipjack tuna larvae from the EPO to the WPO, these authors caution that this tendency is perhaps overstressed due to a potential bias in the data.

Tag release and recapture studies have shown that considerable mixing of skipjack tuna exists in the Pacific Ocean (Hunter et al., 1986). There is a large volume of information on skipjack tuna movements in the western Pacific Ocean (WPO). Although there were numerous long-distance movements of individual tagged skipjack tuna observed, the overall percentage of recoveries having displacements of greater than 200 nmi was only 17% and there are few probable migration routes revealed from the recovery of tagged skipjack tuna (Wild and Hampton, 1994). Furthermore, when considering skipjack tuna on a Pacific-wide basis, particularly the areas of tagging operations in the WPO, it was concluded that skipjack tuna did not appear to migrate toward specific areas for feeding or spawning but appeared to move in more or less random directions within broad limits (Hunter et al., 1986). There have been no recoveries in the EPO from skipjack tuna tagged in the central or WPO. The assumed eastward migration routes of juveniles described in the skipjack tuna migration model (Rothschild, 1965) lack validation, and hypotheses about the energetic advantages of migration to the EPO using the North

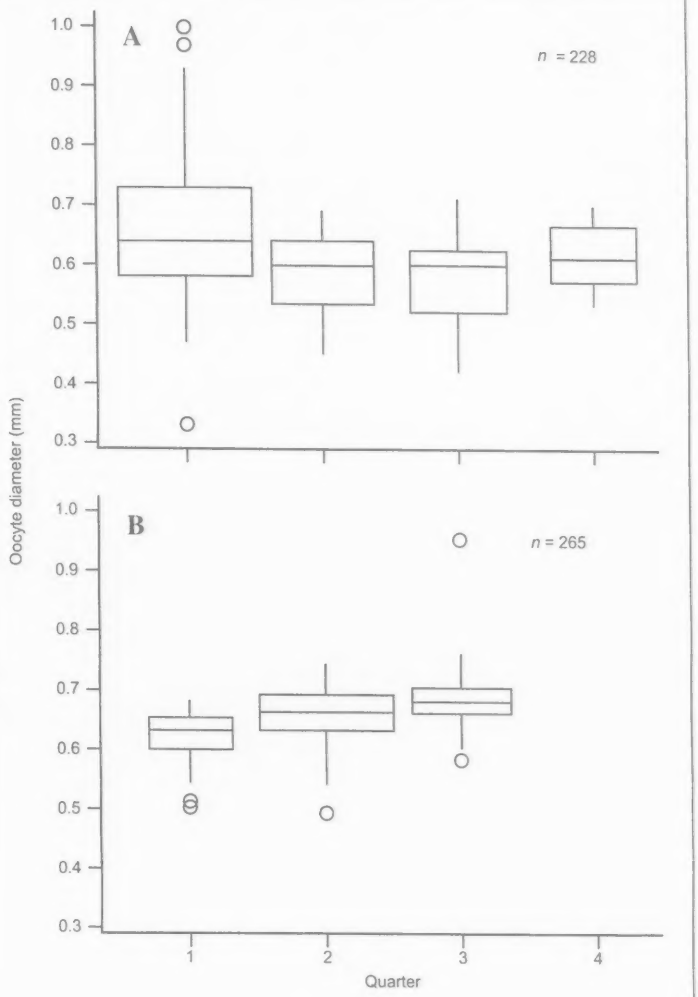

Figure 3

Seasonal variation in oocyte diameters from the most advanced modal group of oocytes from (**A**) skipjack tuna collected from north of the equator and (**B**) skipjack tuna collected from south of the equator during 1995. Immature fish were excluded from this analysis. The width of the box is proportional to the number of samples in the group. The horizontal line within the box is at the median. The bottom of the box is at the first quartile (Q_1) and the top is at the third quartile (Q_3) value. The lines extend from the top and bottom of the box to the adjacent lowest and highest observations within the lower and upper limits defined as $Q_1 \pm 1.5\ (Q_3 - Q_1)$. Outliers are points outside the lower and upper limits and are plotted as circles.

Equatorial Countercurrent and the Equatorial Undercurrent (Williams, 1972) are unsubstantiated.

Numerous tagging studies have also been conducted in the EPO to investigate movements of skipjack tuna (Fink and Bayliff, 1970; Bayliff, 1984). It appears from these studies that skipjack tuna show some consistency of directed movement in the nearshore regions off Central America and northern South America. In the northern region around the Revillagigedo Islands and the west coast of Baja California, there is a northern and then southern movement of the fish between 20°N and 30°N in response to the seasonal movements of the 20°C surface isotherm between about

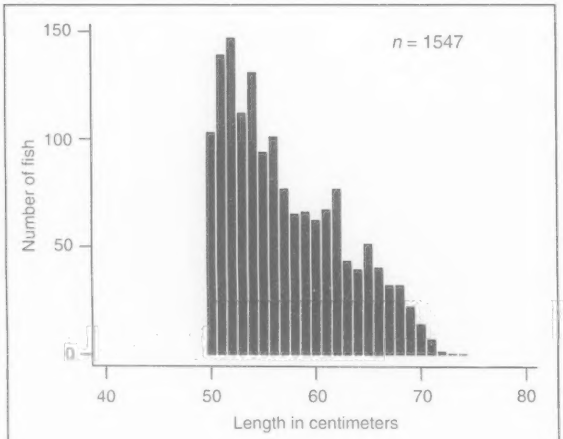

Figure 4

Length distribution for female skipjack tuna sampled in the eastern Pacific Ocean during 1995.

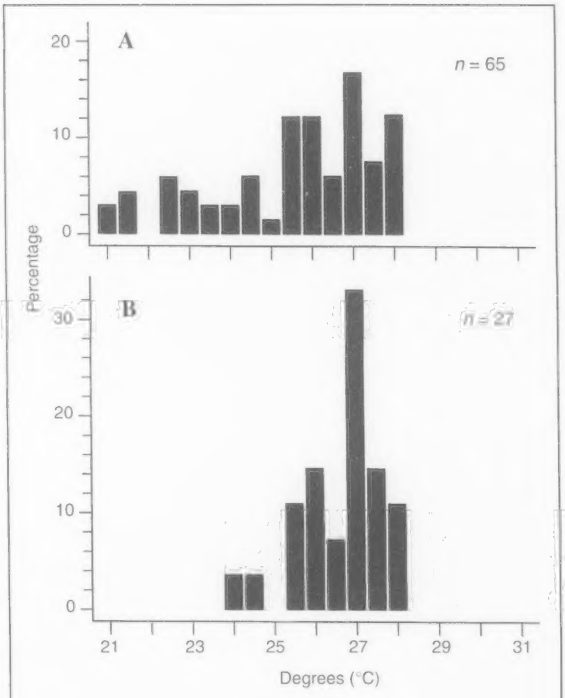

Figure 5

Sea surface temperatures at which (**A**) all skipjack tuna schools were sampled and (**B**) spawning skipjack tuna schools were sampled in the eastern Pacific Ocean during 1995.

May and December. There is also some movement of fish between the northern and southern areas of the fishery in the EPO. However, from well over 100,000 skipjack tuna tagged in the EPO and several thousand returns, only 27 skipjack tuna have been recovered in the central Pacific or the WPO, and 21 of those were recaptured around the Hawaiian Islands (Bayliff, 1988). Of those fish recovered, 19 were tagged off Baja California, 4 fish off the Revillagigedo Islands, 2 fish off Clipperton Island, and 1 fish well offshore at about 4°N and 119°W. Only 1 skipjack tuna tagged in the near shore waters off Central America, within the area of the primary fishery, has been recovered in the central Pacific around Hawaii. Before the recovery of this tagged skipjack tuna there was no evidence from tagging that fish of the southern group migrate to the central Pacific.

Although the information has been largely ignored, morphometrics research has shown significant statistical differences between skipjack tuna from the EPO and the central Pacific (Hawaii and French Polynesia) (Hennemuth, 1959). These differences could indicate a low level of mixing of skipjack tuna populations between the central Pacific and the EPO.

Reliable estimates of the skipjack tuna spawning biomass in the EPO are presently unavailable. However, some indication of the relative abundance of skipjack tuna spawners in the EPO can be derived from considering the estimated total catch of skipjack tuna by length intervals from the surface fishery in the EPO (Fig. 7). It is apparent for 1993 to 1998 that there were significant amounts of skipjack tuna greater than 50 cm in length present in the EPO. These data for skipjack tuna catch by length, combined with the data presented in the present study of spawning activity of skipjack tuna females greater than 50 cm in length, provide strong evidence to support the concept of a significant skipjack tuna spawning biomass in the EPO. It also seems reasonable to consider that the subsequent survivors, resulting from skipjack tuna spawning in the EPO, constitute a significant component of the skipjack tuna population in the EPO.

Skipjack tuna do not appear to be a migratory species such as Pacific, Atlantic, and southern bluefin tunas (*Thunnus orientalis*, *T. thynnus*, and *T. maccoyii*) that have discrete spawning locations (Schaefer, in press). Too much emphasis has been placed on long-range movements of a few tagged skipjack. The tagging data for skipjack tuna only supports extensive offshore–onshore movements as well as north–south movements in the EPO. Based upon what is known about skipjack tuna life history (Matsumoto et al., 1984; Wild and Hampton, 1994), it would seem that skipjack tuna need to be opportunistic in their reproductive strategy, taking advantage of the suitable environment in the EPO. Once skipjack tuna reach sexual maturity, they probably spawn throughout their distribution, whenever water temperatures rise above 24°C.

The long-standing premise that skipjack tuna in the EPO are merely short-term transients, originating from spawning in the central Pacific or WPO, should be seriously reconsidered. This issue has important international management implications. Although the stock in the EPO is not a closed unit, as a result of the highly mobile and op-

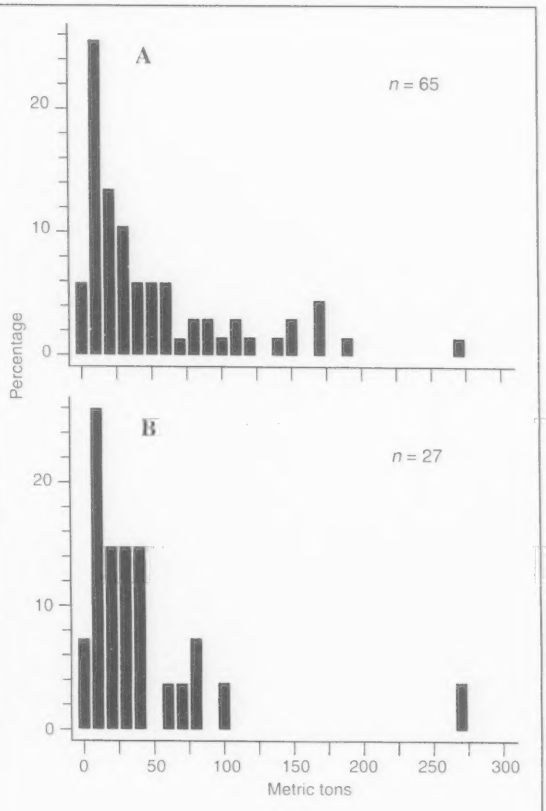

Figure 6

Sizes of (**A**) all skipjack tuna schools sampled and (**B**) those containing spawning females.

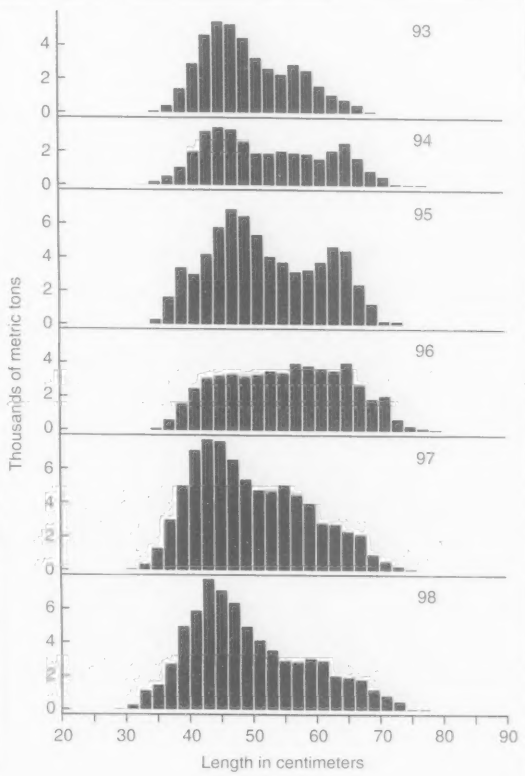

Figure 7

Estimated length compositions of the total skipjack tuna catch, by 2-cm intervals, in the eastern Pacific Ocean. These histograms are based on the catch statistics and length-frequency samples of skipjack tuna, for each year of the 1993–98 period, compiled by the Inter-American Tropical Tuna Commission.

portunistic nature of this species, assessments should nevertheless be conducted for the skipjack tuna stock within this geographical region. Ideally, stock assessment models for skipjack tuna should incorporate spatial and temporal variability in the size-specific parameters for age, growth, movement, mortality, and reproduction. A more comprehensive investigation of the reproductive biology of skipjack tuna in the EPO is in progress.

Acknowledgments

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Biochemical identification of shark fins and fillets from the coastal fisheries in New Zealand

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Abstract—The protein fingerprints of shark fillets and fins taken from commercial landings in northern New Zealand waters were compared with the protein fingerprints from control samples of ten species of coastal sharks. Isoelectric focusing (IEF) in agarose gels revealed species-specific protein profiles in the ten control species. The fillets and fins were identified as school shark (*Galeorhinus galeus*), rig (*Mustelus lenticulatus*), hammerhead shark (*Sphyrna zygaena*), and bronze whaler (*Carcharhinus brachyurus*). Around 40% of fillets from cartons labelled as lemon fish (*M. lenticulatus*) were from other species. Shark fins were identified from four species, two of which are prohibited target species in northern New Zealand. The large number of mislabelled shark products necessitates the use of a simple biochemical technique for identification of shark species in commercial shark products. With IEF, around 100 specimens can be identified by a laboratory technician each working day from small amounts (<0.5 g) of white muscle.

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Several shark species are common in New Zealand coastal waters and form the basis of fisheries producing fillets for the domestic market and fins for the Asian market. Like most sharks, the New Zealand species are vulnerable to over exploitation owing to their slow growth rate, large size at maturity and low fecundity (Castro et al., 1999). Three shark species are currently managed under the New Zealand Quota Management System (QMS): school shark (*Galeorhinus galeus*), rig (*Mustelus lenticulatus*), and the Callorhinchidae elephant fish (*Callorhinchus milii*) (Annala et al.[1]). Quotas were introduced for these species in 1986 following dramatic increases in catches. Two species, *G. galeus* and *M. lenticulatus*, are caught in set-net fisheries that target coastal sharks, and since the introduction of the QMS, the fisheries have stabilized at around 5000 tons per annum (Annala et al.[1]). A competitive quota has been established for spiny dogfish (*Squalus acanthias*), but other species of shark, either because of low abundance or assumed low value, have been excluded from the QMS. Some of these shark species, such as bronze whaler (*Carcharinus brachyurus*), hammerhead shark (*Sphyrna zygaena*), and blue shark (*Prionace glauca*), are taken as bycatch in other fisheries but are prohibited as target species.

The shark species in the New Zealand coastal fisheries are large, and whole fish are readily identified by external characteristics. However most sharks are processed at sea: specimens are "trunked"—the head, guts, and fins are removed—and the product chilled or frozen. Further processing may take place on land and the product is sold as either trunks or fillets and fins. It is difficult to identify fillets and fins to the species level and landed catches may include several species. Management and enforcement of multispecies shark fisheries require that landed products can be correctly identified to the species level. Thus a robust test is needed that will allow identification of fillets and fins.

Several molecular genetic methods have been applied to fisheries-related taxonomic problems to identify and distinguish closely related species. Allozymes have been the primary tool for taxonomic problems in fishes (e.g. Dayton et al., 1994; Lacson and Bassler, 1992) and have revealed cryptic species in teleosts (e.g. Lacson, 1994; Smith et al., 1996). More sophisticated and expensive molecular methods, based on DNA extraction, followed by sequencing or restriction enzyme digestion, are increasingly used for similar identification problems (Bartlett and Davidson 1992), including shark species (e.g. Martin, 1993; Heist and Gold, 1998). Isoelectric focusing (IEF) of muscle proteins has been the preferred method for identification of teleost fillets and products (Lundstrom, 1980; Rehbein, 1990); the method is used in legal cases to identify mislabeled fish products. Polyacrylamide IEF (Lundstrom, 1977, 1980) has been adopted by the U.S. Food and Drug Administration for iden-

[1] Annala, J. H., K. J. Sullivan, C. J. O'Brien, and S .D. Iball. 1998. Report from the Fishery Assessment Plenary, May 1998: stock assessments and yield estimates, 409 p. Unpublished report held in NIWA Library, 301 Evans Bay Parade, Wellington, New Zealand.

Table 1

Common and scientific names of shark control samples used in the isoelectric focusing analyses.

Common name	Other common names	Scientific name
Rig	gummy shark, smoothhound, spotted dogfish, spotted smoothhound, lemon fish, pioke	*Mustelus lenticulatus*
School shark	grey shark, tope, flake, makohuarau, tupere	*Galeorhinus galeus*
Spiny dogfish	southern spiny dogfish, spurdog, spineback, spikey dog	*Squalus acanthias*
Northern spiny dogfish	grey spiny dogfish, shortspine spurdog, green-eyed dogfish	*Squalus mitsukurii*
Hammerhead shark	hammerhead	*Sphyrna zygaena*
Bronze whaler	whaler	*Carcharhinus brachyurus*
Blue shark	blue pointer, blue whaler	*Prionace glauca*
Porbeagle	mackerel shark	*Lamna nasus*
Mako	mackerel shark	*Isurus oxyrinchus*
Carpet shark	swell shark, cat shark	*Cephaloscyllium isabellum*

tification of fish product (Tenge et al., 1993) and applied to shark species (Weaver et al., 1999); it provides a finer separation of proteins than conventional starch and cellulose acetate electrophoresis, and the muscle proteins exhibit little intraspecific variation. In addition, muscle proteins are stable, withstanding repeated freezing and thawing, and provide a species profile in one gel, unlike allozyme methods, where several gels are required in order to identify a range of species. However, some closely related species of teleosts share protein profiles (Bartlett and Davidson, 1991; Smith et al., 1994; Smith et al., 1996) and thus IEF is not always amenable for distinguishing closely related species. Our study was undertaken to evaluate agarose IEF (Lundstrom, 1981, 1983) of shark muscle proteins in order to provide a quick and robust biochemical method to identify shark fins and fillets from commercial vessels and the market place.

Materials and methods

Samples

Control samples were taken from shark specimens caught on research and commercial vessels around New Zealand (Table 1). The specimens were frozen whole at sea and returned to the laboratory where the identity of the species was confirmed through the use of identification keys (Paulin et al., 1989). Samples of white muscle were removed from up to ten specimens of each species. For *Mustelus lenticulatus* and *Galeorhinus galeus*, ten specimens were tested from the Bay of Plenty, North Island, and ten specimens from the east coast South Island. Muscle tissue samples were stored in separate, labelled bags at –70°C. In addition, samples of body muscle from the head, mid, and tail regions were compared with samples of muscle from the base of the pectoral and dorsal fins taken from the same specimens for both *M. lenticulatus* and *Sphyrna zygaena*.

Mustelus lenticulatus and *G. galeus* are in the same family of smoothhounds (Triakidae) and lack the characteristic dorsal spine of the spiny dogfishes. Whole specimens of *M. lenticulatus* are distinguished from *G. galeus* by the size of the second dorsal fin, which is nearly as large as the first dorsal fin in *M. lenticulatus*, but much smaller in *G. galeus*, and by their teeth; there are small teeth or grinding plates in *M. lenticulatus* and distinctive large triangular teeth in *G. galeus* (Paulin et al., 1989). Both species are widely distributed in temperate coastal waters and total recorded landings in New Zealand are around 3200 tons for school shark and 1800 tons for *M. lenticulatus* (Annala et al.[1]). Two species of spiny dogfish (Squalidae) are common in New Zealand waters, the shortspine dogfish (*Squalus mitsukurii*) in northern waters and the spiny dogfish (*Squalus acanthias*) in southern waters. The hammerhead shark (*Sphyrna zygaena*, family Sphyrinidae) was included because small specimens are caught in northern waters of New Zealand. The species has a characteristic black margin to the fins, but we have noted that juvenile, but not adult, *G. galeus* also have a black margin on the dorsal fin. Two species of requiem sharks (family Carcharhinidae), *Carcharhinus brachyurus* and *Prionace glauca*, are also common in coastal waters but are prohibited as target species in northern New Zealand. *Lamna nasus*, *Isurus oxyrinchus*, and *Cephaloscyllium isabellum*, which are caught in northern New Zealand, were also included as controls (Table 1).

Three-hundred and eighty shark fins were supplied by Ministry of Fisheries staff from commercial shark fisheries in the Bay of Plenty in northern New Zealand. In the laboratory, a small piece of muscle tissue was removed from each fin and stored at –70°C. The color and shape of each fin was noted and the maximum length between the flesh area and the fin tip was recorded; fins were stored frozen at –20°C. Eight 10-kg cartons of shark fillets, all labelled as lemon fish (=*M. lenticulatus*), were tested. A small piece of muscle tissue was removed from each individual fillet, labelled, and stored at –70°C prior to isoelectric focusing.

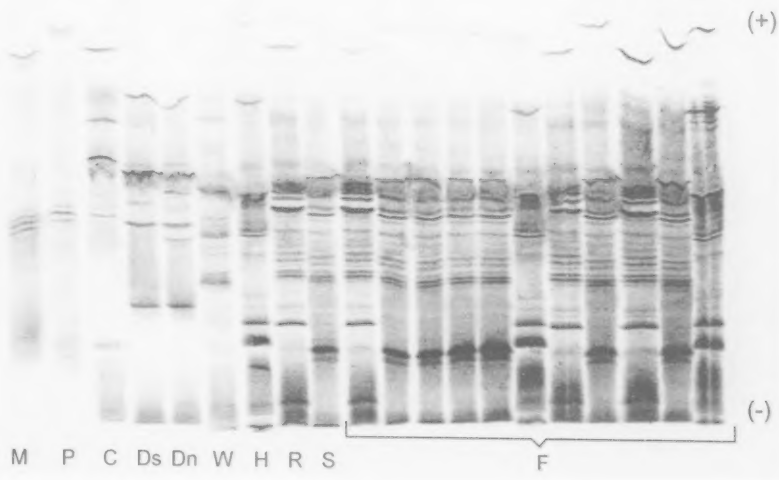

Figure 1

Isoelectric focusing plate of muscle protein fingerprints of nine species of New Zealand sharks and the protein fingerprints of some suspect fillets, all labeled as lemon fish (*M. lenticulatus*). M = *Isurus oxyrinchus*, P = *Lamna nasus*, C = *Cephaloscyllium isabellum*, Ds = *Squalus acanthias*, Dn = *Squalus mitsukurii*, W = *Carcharhinus brachyurus*, H = *Sphyrna zygaena*, R = *Mustelus lenticulatus*, S = *Galeorhinus galeus*, F = fillets labelled as *M. lenticulatus*.

Isoelectric focusing

Small samples (about 0.5 g) of white muscle were removed from each of the tissue samples taken from the fins and fillets and from control samples taken from known specimens of New Zealand shark species. The muscle samples were homogenized individually in two volumes of cold (4°C) deionised water and centrifuged at 12,000 g for five minutes at 4°C. The clear supernatants were placed on filter paper wicks that were placed directly onto agarose IEF gels (Amersham Pharmacia Biotech, Uppsala) on a flat bed IEF system (Amersham Pharmacia Biotech, Uppsala). The 1-mm 1% agarose gels were made up in wide range pharmalyte, pH 3–10 (Amersham Pharmacia Biotech, Uppsala), and focused at 1500 volts for 90 minutes. After focusing, the proteins were fixed, washed, stained with coomassie brilliant blue (BDH Laboratory Supplies, Poole), destained, and dried (Benson and Smith, 1989). An initial gel was run with control samples only to ensure that each species produced a unique protein fingerprint. In addition, samples of body muscle from the head, mid, and tail regions were compared with samples of muscle from the base of pectoral and dorsal fins taken from the same specimens of *M. lenticulatus* and *S. zygaena*. Twenty-five suspect and seven control samples were run on subsequent gels. The same control samples were used in each IEF gel to avoid mismatches between gels.

Results

The muscle tissue samples from the control specimens produced different protein fingerprint patterns in each species (Fig. 1). Tests of samples of body muscle and fin muscle from the same specimen produced the same IEF pattern, demonstrating that the muscle control samples were suitable for identification of fillet or fin samples. Samples of *M. lenticulatus* and *G. galeus* from the Bay of Plenty and east coast South Island showed no intraspecific variation in protein profiles.

The fins could be grouped into three types based on shape: dorsal, pectoral, and caudal (or tail). There was a wide range of sizes from 7 to 28 cm. It is possible that some small dorsal fins may have been anal fins or second dorsal fins. Most fins were of a pale gray color, but some were a darker gray color and had a narrow black margin; most of these latter fins had a narrower shape than the pale gray dorsal fins. A few pectoral fins were dark gray on one surface and light gray on the other surface. None of the fins had a spine or showed sign of a spine having been cut out.

The protein fingerprints of most of the suspect shark fins matched with one of the fingerprint patterns of *M. lenticulatus*, *G. galeus*, *S. zygaena*, or *C. brachyurus* (Table 2). Four of the 392 fins produced a weak and indistinct fingerprint pattern that could not be matched to any of the control samples. Around 10% of the fins were from two spe-

Table 2

Number of shark fins and fillets identified to species level with isoelectric focusing of muscle proteins. All of the fillets were from commercial cartons labeled as lemonfish (*Mustelus lenticulatus*). No ID = not identified because of a weak protein fingerprint.

Fin or fillet	*M. lenticulatus*	*G. galeus*	*S. zygaena*	*C. brachyurus*	No ID
Pectoral fin	127	69	0	7	0
Dorsal fin	81	46	25	3	3
Tail fin	0	6	22	1	1
Unidentified	1	0	0	0	0
Fillet	113	27	28	26	1

cies that are prohibited as target species, *S. zygaena* and *C. brachyurus* (Table 2). None of the protein fingerprints of the fin samples matched with the control samples from *S. mitsukurii*, *S. acanthias*, *P. glauca*, *L. nasus*, *I. oxyrinchus*, or *C. isabellum*.

Protein fingerprints of fillets from cartons labelled as lemon fish (*M. lenticulatus*) showed that the fillets were from four shark species, two of which are prohibited as target species, *S. zygaena* and *C. brachyurus* (Table 2), and that 41.8% of the fillets were not the species shown on the carton labels.

Discussion

To identify the suspect shark fillets and fins, it is essential to use a test that can distinguish closely related species of sharks. Occasionally closely related pairs of species are found with very similar protein fingerprints, e.g. the teleosts tarakihi and king tarakihi, in which case additional biochemical tests are sought to identify specimens (Smith et al., 1996). The muscle tissue samples from the shark control specimens produced different protein fingerprint patterns in each species (Fig 1.). Samples of body muscle and fin muscle from the same specimen produced the same IEF pattern. In addition, samples of *M. lenticulatus* and *G. galeus* from the Bay of Plenty in the North Island and east coast South Island showed no intraspecific variation in protein profiles. These observations demonstrate that muscle protein profiles are an appropriate tool for the identification of shark fillets or fins taken in the New Zealand coastal fishery.

It is not possible to quantify the results and state how many fish specimens have been sampled in the fins and fillets. Each fish may yield two pectoral, two dorsal, one caudal, and one anal fin, but fishermen may discard small or damaged fins. Likewise with fillets, each fish may yield a minimum of two fillets, but four or more fillets may be taken from large specimens. Nevertheless the results indicate that both quota and nonquota species are being landed for the fillet and fin markets, and that the domestic market has cartons of mislabelled species. Around 40% of the fillets tested in our study were not the species on the label—*M. lenticulatus* (Table 2). Such observations demonstrate that shark landings recorded in New Zealand waters may be inaccurate, which will not only confound catch statistics but may compromise assessments upon which regulatory decisions are made. The mislabeled fillets identified in our study suggest that effort is targeting non-ITQ species or that prohibited target species such as *Carcharhinus brachyurus* (prohibited in area 1), and *Sphyrna zygaena* (prohibited in all areas) are being landed.

Unlike other biochemical techniques, such as allozyme and DNA markers, the protein fingerprints revealed by IEF show little intraspecific variation (Lundstrom, 1981). Most individuals from the same species have identical protein fingerprints. When protein fingerprints vary among individuals from the same species, the differences are restricted to the presence or absence of one or a few of the protein bands; the majority of bands are shared among all individuals.

Isoelectric focusing is a relatively quick and cheap identification technique (Lundstrom, 1981) compared with DNA-based extraction methods. One operator is able to process and identify up to 100 specimens in one working day. The IEF technique works well with fresh and frozen material and produces clear protein profiles. However, some proteins denature when they are heat-treated (Keenan and Shaklee, 1985). Therefore, shark products, such as sun-dried fins, may require alternative methods, such as polyacrylamide gel electrophoresis of parvalbumins (Keenan and Shaklee, 1985) or DNA-based methods (Martin, 1993; Heist and Gold, 1998), for species identification.

Acknowledgments

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Reproductive cycle, fecundity, and seasonal distribution of the anglerfish *Lophius litulon* in the East China and Yellow seas

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Abstract—The reproductive cycle, sexual maturity, fecundity, and seasonal distribution of the anglerfish *Lophius litulon* were studied from a total of 989 specimens collected in the East China and Yellow seas between March 1991 and July 1997. Males and females reached 50% sexual maturity at 362 mm TL (age 5.4) and at 567 mm TL (age 6.2), respectively. The histology of the gonads showing seasonal changes in both the gonadosomatic index (GSI) and hepatosomatic index (HSI) are described. Mean GSI of females increases rapidly with ovarian development, whereas mean HSI decreases from the middle of vitellogenesis until the ovaries have fully matured. Segregation of oocytes by size within the ovary suggests that *L. litulon* spawns in batches, which was confirmed by observation of a captive specimen. Batch fecundity (BF) in 15 females with secondary yolk stage ovaries was related to total length (TL, mm) by the equation $BF = (-1.64 \times 10^6) + 3688.13\,TL$ ($546 \leq TL \leq 846$). In September, most specimens of both sexes were collected in the Yellow Sea. Between November and January their distribution extended from the Yellow Sea into the East China Sea. During the spawning season (February to May), sexually immature individuals were collected throughout the East China and Yellow seas, whereas sexually mature individuals were caught only in the East China Sea and the coastal waters off Kyushu Island, Japan. The spawning grounds of *L. litulon* extend widely from waters of the East China Sea to inshore waters of Kyushu.

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The anglerfish *Lophius litulon* (Jordan) is distributed throughout Japanese waters, in the Gulf of Po-Hai and the East China and Yellow seas (Caruso, 1983; Yamada, 1986; Yoneda et al., 1997). In Japan, this species and a second anglerfish, *Lophiomus setigerus* (Vahl), are consumed as food, and their livers are considered a delicacy. Both species are caught throughout their range by Japanese, Chinese, and Korean trawl fisheries, primarily during winter months when these fish command a high market price. The catch of anglerfish is very small compared to that of other commercially important species in Japan. Anecdotal evidence from fishermen suggests that catches have declined in recent years, although no official landings are reported. The shallow East China and Yellow seas are subject to intense fishing pressure and large anglerfish, especially *L. litulon*, have become particularly scarce.

In spite of their commercial importance, little biological information is available on *L. litulon* and *L. setigerus*. Kosaka (1966) described age, growth, spawning season, and feeding habits of *L. litulon* in Sendai Bay, off the northeast coast of Honshu Island, Japan; Yamada (1986) reported the spawning season and size at maturity for *L. litulon* and the spawning season for *L. setigerus* in the East China and Yellow seas. Recently we reported the reproductive biology of *L. setigerus* (Yoneda et al., 1998a, 1998c) and age and growth of *L. litulon* (Yoneda et al., 1997) and *L. setigerus* (Yoneda et al., 1998b).

According to Yamada (1986) and Tokimura,[1] the distribution of *L. litulon*

[1] Tokimura, M. 1992. Distribution of primary bottom-fishes in the East China and Yellow Seas during the winter of 1991. Seikai Block Sokouo Chosa Kenkyu Kaiho. 3:15–39 [In Japanese.] Seikai National Fisheries Research Institute, Kokubu, Nagasaki 850-0951, Japan.

varies seasonally: in summer it is found mainly in the Yellow Sea, and during winter and spring it extends its range into the East China Sea. Our study was initiated to examine the role of reproductive biology during the seasonal change in anglerfish distribution and to provide scientific background for a national management policy for the anglerfish fishery.

Materials and methods

A total of 989 specimens (males=549, females=412, unknown sex=28), caught between March 1991 and July 1997, were examined (Fig. 1). Of these, 529 specimens were obtained from five trawl surveys conducted by the Seikai National Fisheries Research Institute (SNFRI). A further 425 specimens were bought in fish markets at Shimonoseki, Fukuoka, and Nagasaki, where there are commercial landing sites. The locations and date of capture of these fish were obtained from fishermen. The remainder (n=35) were caught during a benthic trawl survey conducted by Nagasaki University.

Five SNFRI benthic trawl surveys between January and February in 1991, 1995, 1996, and 1997, and in September 1993 were conducted in the East China and Yellow seas, between latitudes 27° and 37°30′N, west of 128°E longitude. The sampling area was divided into five regions by using lines of latitude and longitude, and further divided into 30′ × 30′ (minutes) sampling stations (Fig. 1). Eighty and sixty-nine trawl stations were established in the sampling area in 1991 and 1993, respectively, at depths between 35 and 150 m. In 1995, 1996, and 1997, respective totals of 65, 123, and 78 trawl stations were established in the sampling area at depths between 50 and 200 m. All SNFRI surveys were conducted with the RV *Kaiho Maru*, a 466-ton stern trawler. At each station, a bottom trawl, with a 66-mm codend mesh, was towed for 30 minutes at approximately 3 knots. The net mouth was approximately 20 m wide and 5 m high. Nagasaki University conducted a trawl survey in the East China Sea between 29°and 32°N latitude and 126° and 127°30′E longitude, at depths between 70 and 120 m in May 1995 with the training ship *Nagasaki Maru*, an 842-ton stern trawler. Seventeen sampling stations were established. A bottom trawl net, with a 62-mm codend mesh, was towed for 60 minutes at approximately 3 knots. The net mouth was approximately 17 m wide and 10 m high. Most specimens captured by the commercial fishery were obtained in winter and spring because the fishing areas of commercial vessels vary seasonally owing to seasonal changes in the target fishes. Winter and spring specimens were available from the southern Yellow Sea to the northern East China Sea, between latitudes of approximately 30° and 35°N, west of 128°30′N, at depths between 35 and 200 m, and were supplemented with specimens from the coastal waters of northern Kyushu Island, Japan. Summer and fall specimens were taken from the East China Sea, roughly between latitudes 28° and 33°N, west of 128°30′N, at depths between 35 and 200 m.

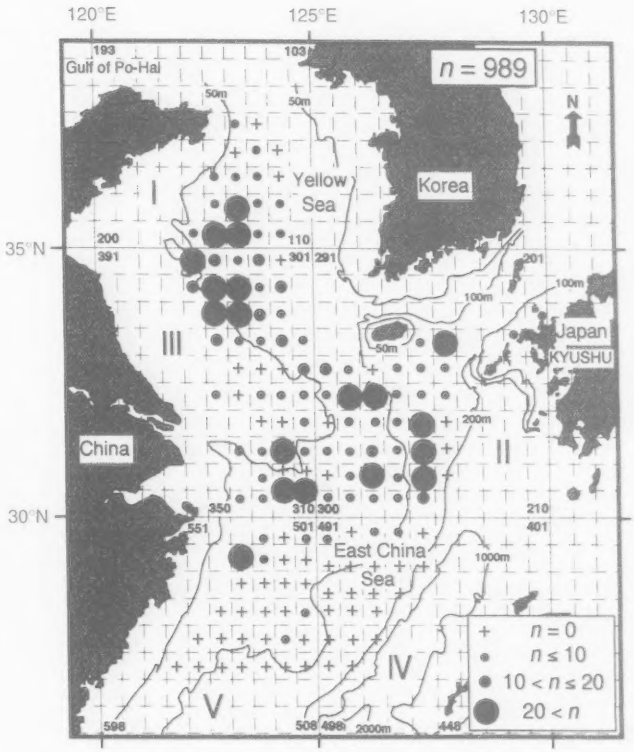

Figure 1

Geographical distribution of specimens of *Lophius litulon* collected in the East China and Yellow seas. Roman numeral (I–V) represents each sampling area. Arabic numeral represents the sampling station number. n = total number of fish examined.

The total length (TL) of all specimens was measured to the nearest millimeter. Body weight (BW) and visceral weight (VW) were determined to the nearest gram, and gonadal weight (GW) and liver weight (LW) were measured to the nearest 0.1 g. From 989 specimens measured during this study, 367 testes and 267 ovaries were collected. For histological examination, the middle portion of the left testicular lobe was excised, as well as three different parts of the ovary (the center of the anterior, middle, and posterior portions of the left ovarian lobe). These tissue samples were fixed in Bouin's fluid for 24 hours and preserved in 70% ethanol. The remainder of each ovary was preserved in 10% formalin to measure oocyte size (diameter, size-frequency distribution, and batch fecundity) because oocytes shrink when fixed in Bouin's fluid.

After dehydration in ethanol, the gonadal tissues were embedded in paraffin wax or methacrylate polymer resin (Technovit, Kulzer). Paraffin sections, 5–10 µm thick, were stained with Mayer's haematoxylin-eosin. Methacrylate polymer resin sections, 2–3 µm thick, were stained with a 1% solution of toluidine blue. Paraffin serial sections

Table 1

Histological characteristics of oocytes at different developmental stages in *Lophius litulon*.

Developmental stage of the oocyte	Oocyte diameter (μm)	Histological characteristics
chromatin nucleus	less than 20	Nucleus has a large nucleolus.
perinucleus	35–160	Multiple nucleoli are seen toward the periphery of the nucleus; oil droplets appear around the nucleus and increase in number; follicle cells surrounding the oocyte have formed a narrow layer.
yolk vesicle	180–250	Yolk vesicles appear in the peripheral region of the cytoplasm.
primary yolk	300–530	Yolk globules appear between the yolk vesicles and increase in number; both granulosa and thecal cell layers are clearly observed.
secondary yolk	480–730	Oocytes are larger and yolk globules fill the cytoplasm.
tertiary yolk	750–1000	Yolk accumulation progresses rapidly, which results in a marked increase in the size of oocytes.
migratory nucleus	950–1300	Yolk globules begin to fuse with one another; oil droplets fuse to form larger ones.
mature	1450–1700	After germinal vesicle breakdown, yolk globules form a single mass and oil droplets coalesce to form larger ones.
atretic	—	Early: disintegration of the nucleus and yolk globules and hypertrophy of the follicular cell layers.
		Late: presence or absence of intercellular vacuoles, flocculent material, and granular pigments.

were mainly used for observations of whole gonadal structure, whereas polymer resin sections were used for detailed observations of oocyte development, spermatogenesis, and the definition of gonadal stages. In our study, polymer resin sections fixed in Bouin's fluid gave the best results. The developmental stages of the oocytes were categorized according to Yamamoto (1956) and Yoneda et al. (1998a) (Table 1). Histological classification of atretic oocytes (Table 1) and postovulatory follicles followed Hunter and Macewicz (1985) and Yoneda et al. (1998a). Only specimens larger than the minimum size at sexual maturity (see "Results" section) were used to examine seasonal changes in gonadal condition.

Oocyte diameter was measured with a profile projector (20–100×), and the range was determined by using the largest and smallest oocytes in the whole projected field from each developmental oocyte stage. Oocyte diameter at each developmental stage was measured in the following manner: the developmental stage of the most advanced oocytes in each ovary was identified from histological sections, and the diameters of 50 formalin-fixed oocytes forming the largest size class in ovaries at each developmental stage were measured (one or two randomly selected specimens).

Because the arrangement of oocytes shows a gradation in developmental stage within each ovigerous lamella (see "Results" section), the composition of oocytes within each ovigerous lamella was considered to be the unit within the ovary. To determine the size-frequency distribution of oocytes within each ovarian stage, 50–80 formalin-fixed ovigerous lamellae samples (corresponding to 300–550 oocytes) from each ovarian stage were examined. All oocytes ≥100 μm in yolk vesicle stage ovaries were measured; in other ovarian stages, only oocytes ≥200 μm were measured. The size-frequency distribution of oocytes at each stage represented the ovary from one randomly selected specimen.

Estimates of size at sexual maturity were based on the examination of males (193–692 mm TL [n=236]) and females (174–1013 mm TL [n=246]) collected during the spawning season between February and May. Of these, 38 females were defined as sexually immature, based on macroscopic observations (Afonso-Dias and Hislop, 1996). The remaining 444 specimens were classified into each gonadal stage on the basis of histological observations. Sexually mature individuals were defined as males with testes in stages 3 and 4, and females with ovaries in mid-stage 2 (oocytes at the secondary yolk stage) or at more advanced stages (see Results). Males with testes in stages 3 and 4 collected in the spawning season were thought to have the potential to spawn because our preliminary observations indicated that milt ran from their genital pores on slight pressure. Females with ovaries with secondary yolk stage oocytes were considered sexually mature because an advanced group of secondary yolk stage oocytes forms an isolated batch and increases in size in tandem with ovarian development. Females with ovaries in stages 2 (late), 3, 4, or 5 were also considered sexually mature, because these individuals were thought to be pre- or postspawning fish. Similarly, to estimate age at sexual maturity, the age of individual fish collected in the spawning season was determined by counting the annual ring marks on the surface of the vertebral centrum (Yoneda et al., 1997). Of 482 spec-

Table 2

Summary of results of oocyte density (the number of secondary yolk stage oocytes per unit sample weight [g]) in the ovaries of five female *Lophius litulon* from various locations and results of two-way analysis of variance. int. = interior; ext. = exterior.

	Position of sample in ovary*					
	Right ovary			Left ovary		
TL (mm)	Anterior (int. or ext.)	Middle (center)	Posterior (int. or ext.)	Anterior (int. or ext.)	Middle (center)	Posterior (int. or ext.)
546	2832^{ext}	2711	2802^{ext}	2768^{int}	2960	3000^{int}
647	3008^{ext}	3113	3067^{int}	3059^{int}	3160	2980^{ext}
662	2917^{ext}	3009	2759^{int}	2913^{int}	2635	3216^{ext}
796	2540^{int}	2771	2691^{ext}	2662^{ext}	2990	2780^{int}
847	2607^{int}	2572	2821^{int}	2680^{ext}	2800	2800^{ext}
Mean	2781	2835	2828	2816	2909	2955

	Two-way analysis of variance			
Source of variation	df	SS	MS	*F*
Right vs. left ovary	1	23130	23130	0.73
Position within ovary	2	105500	52730	1.66
Interaction	2	48140	24070	0.76
Error	24	764700	31860	

imens collected in the spawning season, 410 specimens (187 males and 223 females) were used to estimate age at sexual maturity. The vertebral centra of the other 72 specimens were either damaged in preparation or lost. To estimate the total length (L_{50}) and age at which 50% of males and females are sexually mature, the fraction of mature fish in each interval (10-mm length or year of age) was fitted with a logistic function with the Marquardt method (Draper and Smith, 1966).

All specimens $TL \geq L_{50}$ were used to determine the monthly changes in gonadosomatic index (GSI) and hepatosomatic index (HIS) for adult males and females. The GSI and HSI were calculated in the following manner:

$$GSI = (GW / (BW - VW)) \times 100.$$

$$HSI = (LW / (BW - VW)) \times 100.$$

The Kruskal-Wallis test (one-way analysis of variance, ANOVA) followed by Dunn's multiple comparison test were used to test for significant differences between the GSI and HSI values of gonadal stage groups of fish.

Estimation of batch fecundity followed Yoneda et al. (1998a). Batch fecundity was estimated only from specimens with ovaries containing oocytes in the secondary yolk stage and no gelatinous material. Only 15 females contained such ovaries during our study; these fish were thought to be ready to spawn for the first time during that spawning season because their ovaries contained neither postovulatory follicles nor atretic oocytes. To determine whether secondary yolk stage oocytes were randomly distributed throughout the ovary, densities (no. oocytes/g ovary wt.) of secondary yolk stage oocytes from the six locations within the ovaries of five fish were compared (Table 2): two samples from the center of the right and left ovarian lobes, two samples from the posterior section (either from the interior or exterior) and two samples from the anterior section (either from the interior or exterior). A two-way ANOVA was performed to test for the effect of sample location on oocyte density within each ovary. There was no significant change in oocyte density by location of oocytes within the ovaries (Table 2). Advanced yolked (secondary yolk stage) oocytes were randomly distributed within the ovary and samples could be taken from any location without bias. Fecundity samples were collected from six different parts of the ovary, in the anterior, middle, and posterior portion of each ovarian lobe. Ovarian tissue samples (30–120 mg), each containing approximately 100–350 oocytes, were placed on a slide in water and covered with a cover slip. The most advanced oocytes were counted with a profile projector (50–100×). Batch fecundity for each female was calculated as the product of the number of secondary yolk stage oocytes per unit of weight (of each of the six sampling sites) multiplied by the total ovarian weight. Linear regression analysis was used to examine the relationship between batch fecundity and the total length of the fish.

To examine the seasonal distribution of fish, the numbers of specimens collected at each sampling station during each of the three study periods (September, November–January, and February–May) were compared. The September samples were collected in the 1993 SNFRI trawl survey. Samples for the other two periods came from

the trawl surveys conducted by SNFRI between January and February in 1991, 1995, 1996, and 1997, and from the commercial trawl fishery in 1991–97. Additional samples for February–May were collected in the trawl survey conducted by Nagasaki University in May 1995. Sexually mature individuals collected in September and November–January were defined as those larger than the L_{50} for that sex because most had recrudescent gonads. Between February and May, sexually mature individuals were defined as males with testes in stage 4 and females with ovaries in stages 2 (late), 3, 4, or 5 (see "Results" section). These individuals were thought to be pre- or postspawning fish, possibly collected at or near the spawning grounds. Sexually immature individuals were defined as males with testes in stages 1 or 2 and females with ovaries in stage 1. These individuals were considered to be nonspawning fishes present during the spawning season.

Results

Structure of the testis

The paired testicular lobes are located in the posterior portion of the abdominal cavity. The main longitudinal sperm duct is located ventral to the testicular groove (hilus) in each testis. The seminiferous tubules radiate towards and terminate blindly from the testicular periphery of the main sperm duct. The germinal cysts of spermatogonia, spermatocytes, and young spermatids are arranged randomly on the walls of the seminiferous tubules (Fig. 2A). As young spermatids mature, they are released from their cysts into the lumina of the seminiferous tubules (Fig. 2B). Spermatids and spermatozoa are both found in the lumina of the seminiferous tubules and sperm ducts (Fig. 2, B and C).

Structure of the ovary

The right and left ovarian lobes of *L. litulon* are connected to each other at their posterior ends, forming a single organ. Stalk-like ovigerous lamellae protrude from the ovarian wall and each contains many oocytes at different stages of development. In developing and maturing ovaries, one or two of the most advanced oocytes are located in the terminal portion of each ovigerous lamella, and previtellogenic oocytes are found near the base of the ovigerous lamella throughout the year.

The ovarian lumen is lined with both ovarian wall epithelium and ovigerous lamella epithelium. These epithelia undergo morphological changes accompanying the ovarian maturation cycle (Fig. 3). As ovarian development continues in the secondary and tertiary yolk stages, gelatinous material is secreted from both the ovigerous lamellar epithelium and ovarian wall epithelium, and fills the ovarian lumen.

The early-stage postovulatory follicles are convoluted, with many folds, and contain a follicular lumen (Fig. 4A). The granulosa cells are either columnar or cuboidal and are arranged in a regular manner together with thecal cells (Fig. 4B). The nuclei are located in the basal or middle portion of the granulosa cells. The late-stage postovulatory follicles are much smaller than those in the previous stage, and the follicular lumen continues to decrease

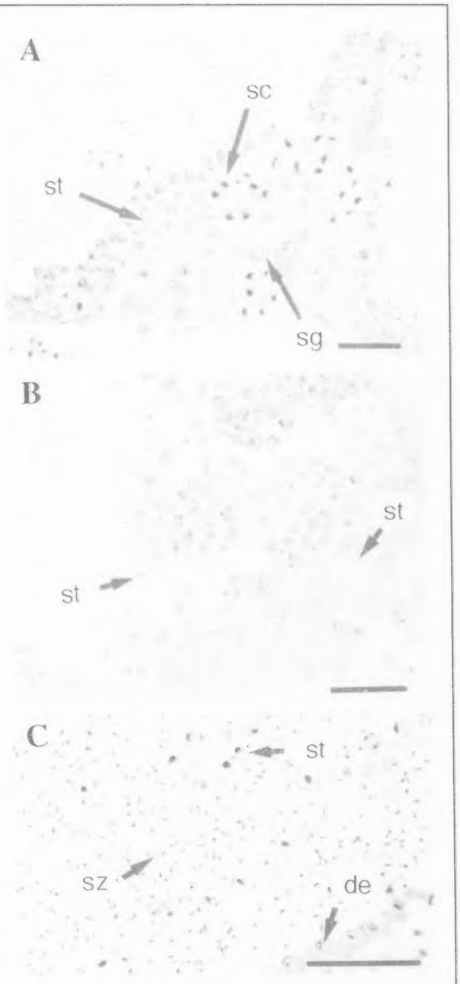

Figure 2

Photomicrographs of sections of the testis of *Lophius litulon*. (**A**) Transverse sections of the seminiferous tubules during spermatogenesis, showing that the germinal cysts are arranged randomly on the walls of the seminiferous tubules. (**B**) Transverse sections of the seminiferous tubules during spermatogenesis, showing that spermatids are released into the lumina of the seminiferous tubules. (**C**) Transverse section of the main sperm duct during spermatogenesis, showing that both spermatids and spermatozoa are present in the main sperm duct. Bar = 25 μm; sg = spermatogonia; sc = spermatocyte; st = spermatid; sz = spermatozoon; de = main duct epithelium.

in size until it disappears (Fig. 4C). Ultimately, the granulosa cell layer becomes indistinct and the thecal cell layer is much regressed.

Maturity stages of testes

The testes can be classified into four stages of maturity according to their histological characteristics. No spent specimens, defined as those in which spermatogenesis has ceased and residual spermatozoa remain in the testis, were found during the study.

Stage 1 immature (Fig. 5A): Germinal cysts containing spermatogonia, spermatocytes, and spermatids are observed along the wall of the seminiferous tubules. Spermatids and spermatozoa are not present in the lumina of the seminiferous tubules and the small main duct. All specimens with testes at this stage were ≤306 mm TL.

Stage 2 early spermatogenesis (Fig. 5B): Germ cells at all stages of spermatogenesis are present. Spermatids and a few spermatozoa are observed in the lumina of the seminiferous tubules and main sperm duct.

Stage 3 late spermatogenesis (Fig. 5C): Active spermatogenesis occurs in the testes. Spermatids and spermatozoa are more abundant in the lumina of the seminiferous tubules and in the main sperm duct than in the previous stage.

Stage 4 mature (Fig. 5D): Large quantities of spermatozoa and a few spermatids are present in the lumina of the seminiferous tubules and main sperm duct. Spermatogenesis and spermatogonial division also occurs in the seminiferous tubules, though few, if any, germinal cysts containing spermatogonia or spermatocytes are found around the main sperm duct.

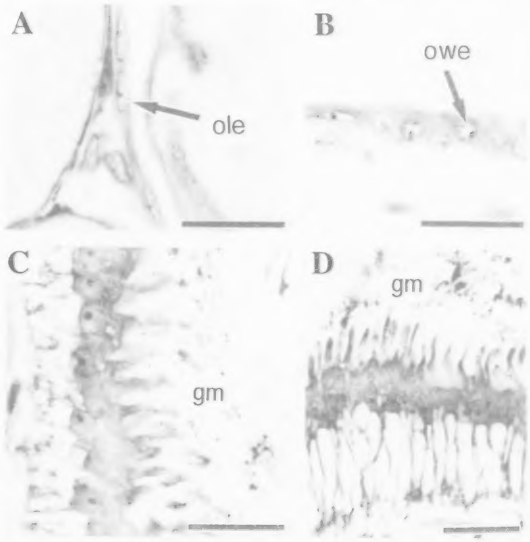

Figure 3

Photomicrographs of the ovigerous lamellar epithelium and ovarian wall epithelium at various stages of ovarian maturation in *Lophius litulon*. (**A**) Ovigerous lamellar epithelium (ole) at the previtellogenic stage. (**B**) Ovarian wall epithelium (owe) at the previtellogenic stage. (A) and (B) show the epithelial cells of both the ovigerous lamella and ovarian wall are squamous or cuboidal in shape and contain a small nucleus. (**C**) Ovigerous lamellar epithelium at the tertiary yolk stage. (**D**) Ovarian wall epithelium at the tertiary yolk stage. (C) and (D) show that gelatinous material is actively secreted from the apical surfaces of the epithelia of both the ovigerous lamellae and ovarian wall. Bar = 25 µm; gm = gelatinous material.

Maturity stages of ovaries

The ovaries can be classified into six stages of maturity according to their histological characteristics and the development of the most advanced oocytes. The classification of stage-4, -5, and -6 ovaries is based on a modification of the atretic states of Hunter and Macewicz (1985).

Stage 1 immature (Fig. 6A): Only previtellogenic oocytes are present and the epithelia of both the ovigerous lamellae and ovarian wall are thin.

Stage 2 developing (Fig. 6B): Most advanced oocytes have reached the primary to tertiary yolk stages. All of the ovigerous lamellae have vitellogenic oocytes. This stage can be subdivided into early and late stages. The early stage is defined by the presence of primary or secondary yolk stage oocytes and the late stage by the presence of tertiary yolk stage oocytes with gelatinous material.

Stage 3 mature (Fig. 6C): The most advanced oocytes are in the migratory nucleus or mature stages. The ovulated oocytes are found in the gelatinous material forming within the ovarian lumen just before spawning. A part of the remaining smaller oocytes contains early yolk stage oocytes.

Stage 4 spawning (Fig. 6D): Vitellogenic oocytes with no sign of atresia and postovulatory follicles are present. Degenerating residual mature oocytes are frequently observed. More than 50% of the ovigerous lamellae have vitellogenic oocytes.

Stage 5 spent (Fig. 6E): Vitellogenic oocytes are degenerating (early atretic stage) and postovulatory follicles are observed. More than 50% of the ovigerous lamellae have only previtellogenic oocytes or atretic oocytes (or both).

Stage 6 resting (Fig. 6F): Late atretic stage oocytes and previtellogenic oocytes are present, and the epithelia of both the ovigerous lamellae and ovarian wall are thin.

To determine how frequently ovigerous lamellae were found with yolked oocytes after spawning, 30–50 ovigerous lamella samples from the ovaries of 18 females with

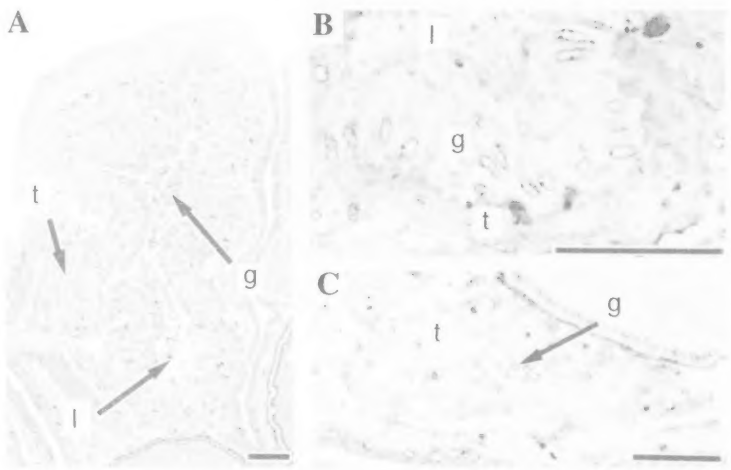

Figure 4

Photomicrographs of atretic postovulatory follicles of *Lophius litulon*. (**A**) and (**B**) Early-stage postovulatory follicles. (B) shows that the granulosa cells are arranged in an orderly manner together with the thecal cells. (**C**) Late-stage postovulatory follicles. Bar = 75 µm; l = follicular lumen; g = granulosa cell layer; t = thecal cell layer.

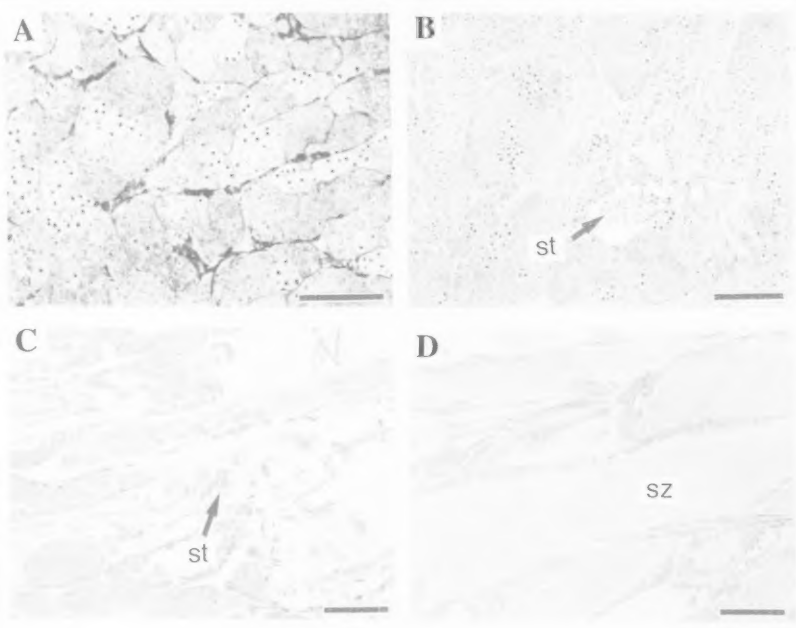

Figure 5

Photomicrographs of testes in the four different stages of maturity in *Lophius litulon*. (**A**) Stage 1 (immature). (**B**) Stage 2 (early spermatogenesis). (**C**) Stage 3 (late spermatogenesis). (**D**) Stage 4 (mature). Bar = 100 µm; st = spermatid; sz = spermatozoon.

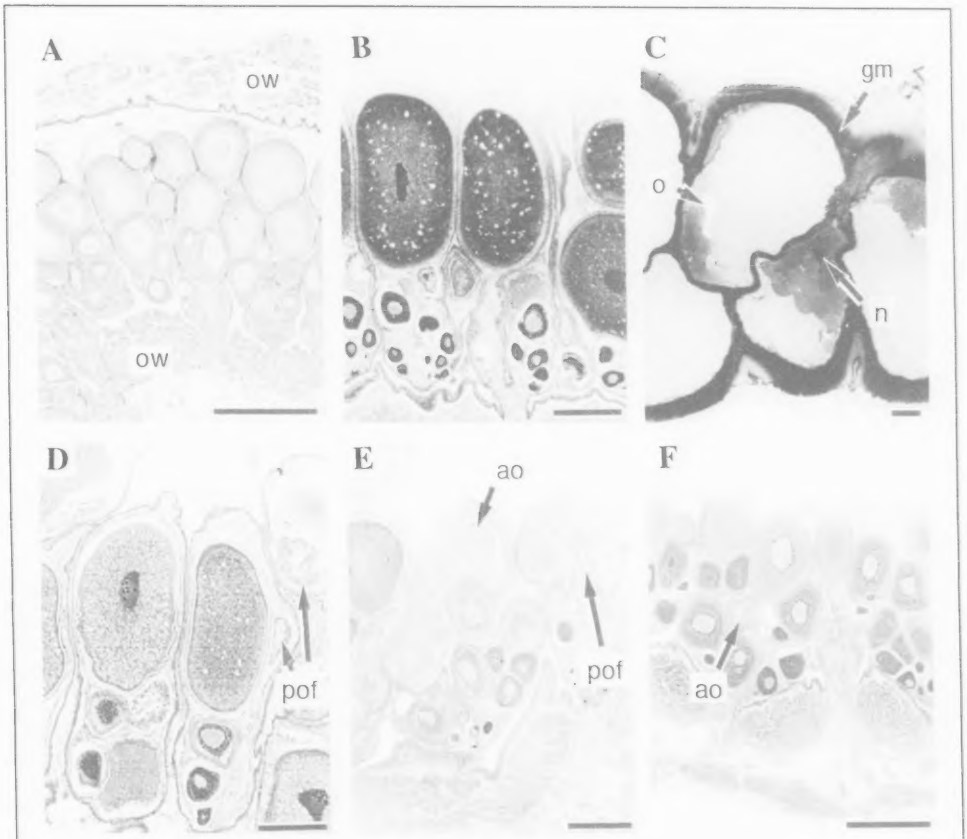

Figure 6

Photomicrographs of ovaries at the six different stages of maturity in *Lophius litulon*. (**A**) Stage 1 (immature). (**B**) Stage 2 (developing). (**C**) Stage 3 (mature). (**D**) Stage 4 (spawning). (**E**) Stage 5 (spent). (**F**) Stage 6 (resting). Bar = 250 µm; ow = ovarian wall; gm = gelatinous material; n = nucleus; o = oil droplet; pof = postovulatory follicle; ao = atretic oocyte.

postovulatory follicles were examined. The frequency of ovigerous lamellae with yolked oocytes present clearly differentiates two ovarian conditions (Table 3). The ovaries of females in which more than 75.0% of the ovigerous lamellae have secondary yolk stage oocytes are in stage 4, regardless of the degenerative stage of the postovulatory follicles. The ovaries of females in which less than 36.4% of the ovigerous lamellae have primary yolk stage oocytes are in stage 5. Some yolked oocytes in the process of becoming atretic are found in specimens with primary yolk oocytes. No females were found with ovaries containing both postovulatory follicles and tertiary yolk or a more advanced stage of oocytes during our study.

Length and age at sexual maturity

There were clear differences between males and females in the size and age at sexual maturity (Fig. 7). The minimum size and age at sexual maturity for males were 325 mm TL and age 4; for females, minimum size and age at sexual maturity were 546 mm TL and age 5. The size and age at 50% sexual maturity for males and females were 362 mm TL and age 5.4, and 567 mm TL and age 6.2, respectively. All males ≥390 mm TL and age 7, and all females ≥630 mm TL and age 8, were mature.

Annual reproductive cycle

Mature males were found over a longer period of the year than mature females (Tables 4 and 5). Spermatogenesis occurs throughout most of the year; therefore males with mature testes are frequently collected. In females, early stages of oocyte development occur between November and March, and the later stages from February through April. Females in stages 3 and 4 were collected from February to May, which is therefore considered the spawning season. Between May and November, most females had stage 1, 5, or 6 ovaries.

Table 3

Results of histological examination of stage-4 and stage-5 ovaries of *Lophius litulon* collected between February and June. Stage-4 ovaries are defined as those in which more than 50% of the ovigerous lamellae have yolked oocytes in females with secondary yolk stage oocytes with no sign of atresia, regardless of the degenerative stage of the postovulatory (POF) follicles. Stage-5 ovaries are defined as those in which less than 50% (or none) of the ovigerous lamellae have yolked oocytes with frequent signs of atresia. GSI = gonadosomatic index.

Date	Total length (mm)	GSI	Oocyte stage[1]	POF stage[2]	Ovigerous lamellae with yolked oocytes (%)	Atretic stage[3]	Ovarian stage
27 Feb 93	594	9.14	sy	l	75.0	—	4
20 Mar 95	634	7.00	sy	l	89.7	—	4
20 Mar 95	738	7.50	sy	l	93.0	—	4[4]
18 Mar 96	622	5.31	py	e	30.4	—	5
18 Mar 96	639	4.50	py	l	17.6	e	5
18 Mar 96	711	6.96	sy	l	97.7	—	4
18 Mar 96	1013	6.02	sy	l	92.1	—	4
17 Mar 97	821	6.81	py	e	20.6	—	5
17 Mar 97	853	5.76	py	e	25.0	—	5
26 Apr 94	645	8.30	py	l	20.0	e	5
14 Apr 95	857	8.60	py	l	16.4	e	5
23 Apr 96	702	6.38	sy	e	92.3	—	4
26 Apr 97	868	8.45	py	l	30.8	e	5
5 May 93	626	6.48	sy	e	77.6	—	4
28 May 94	891	7.70	py	l	18.2	e	5
28 May 94	981	9.20	py	l	36.4	e	5
7 May 97	825	3.47	yv	l	0	e, l	5[4]
7 Jun 97	830	4.20	yv	l	0	e, l	5

[1] Most advanced oocytes are py = primary yolk stage; sy = secondary yolk stage; and yv = yolk vesicle stage.

[2] Postovulatory follicles are e = early stage; l = late stage.

[3] Atretic oocytes are e = early stage; l = late stage.

[4] Photographs of histological sections of stage-4 and stage-5 ovaries are shown in Figure 6 (D and E).

Gonadosomatic and hepatosomatic index

The mean GSI for males increased from September and peaked in January after which it declined (Fig. 8A). The mean HSI for males was highly variable between September and December but gradually decreased from January through July (Fig. 8B). The mean GSI for females increased gradually throughout the early part of the year, peaking sharply in May, after which it dropped rapidly (Fig. 8C). The mean HSI for females started to increase in August and peaked in December (Fig. 8D). It remained low between March and July.

With testicular development, the GSI increased and reached a maximum when the testes were in stage 4 (Table 6). There were significant differences in the value of these indices in the stage-4 testes, compared with those in the other three stages ($P<0.05$). The mean HSI for males peaked in stage-1 testes, but there were no statistical differences in the value of the median HSI between the four stages (ANOVA, $P>0.05$).

In females, the mean GSI gradually increased and peaked in stage-3 ovaries (Table 7), but there were no statistical differences in the value of the median GSI between the early stage-2 and stage-5 ovaries ($P>0.05$). The mean HSI peaked in early stage-2 ovaries and then dropped rapidly with ovarian development. The median HSI during the early and late stage-2 ovaries was significantly higher than in stage-1, stage-3, and stage-5 ovaries ($P<0.05$).

Size-frequency distribution of oocytes

The size of all the oocytes in a group gradually increased in tandem with ovarian development (Fig. 9). When an advanced group of the oocytes reached the secondary yolk stage, they formed an isolated batch that separated almost completely from adjacent groups of smaller oocytes. Between the tertiary yolk and mature ovary stages, only the oocytes in the advanced batch increased in size, and the remainder of the group remained smaller than 550 µm. This finding would suggest that *L. litulon* is a batch spawner (a conclusion which has been supported by aquarium observations—see "Discussion" section).

Batch fecundity

The relationship between batch fecundity (BF) and total length (TL), based on 15 specimens with secondary yolk

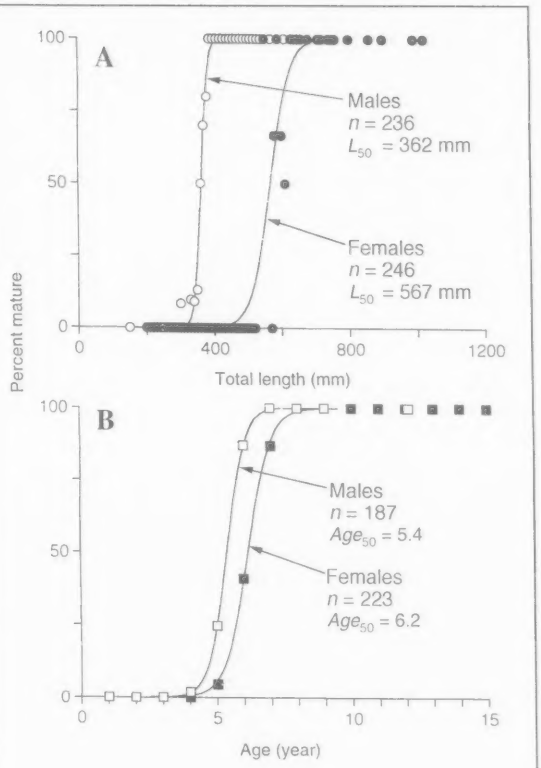

Figure 7

Percent mature fish by size (10-mm length intervals) (**A**) and age (years) (**B**) fitted by a logistic function for male (open circles) and female (solid circles) *Lophius litulon* collected during the spawning season, February through May. n = total number of fish examined; L_{50} = total length at 50% sexual maturity; Age_{50} = age at 50% sexual maturity.

stage ovaries collected between December and February, was described by the equation

$$BF = (-1.64 \times 10^6) + 3688.13\ TL$$

for total lengths between 546 and 846 mm (r^2=0.86; P<0.001) (Fig. 10). Batch fecundity ranged from 0.31×10^6 eggs in a 578-mm-TL fish, to 1.54×10^6 eggs in a 796-mm-TL fish.

Seasonal distribution

In September, most of the specimens from both sexes were collected in the Yellow Sea (Fig. 11). Between November and January their distribution extended from the Yellow Sea to the East China Sea. At this time, sampling sites showed a clear difference in the distribution of sexually mature males and females. Males were collected mainly in the East China Sea, whereas females were collected only in the Yellow Sea. During the spawning season, from February throughout May, immature individuals were collected throughout the East China and Yellow seas, whereas mature individuals were caught only in the East China Sea and the coastal waters off Kyushu, and none were caught in the Yellow Sea.

Table 4

Number of males *Lophius litulon* in the East China and Yellow seas at the various maturity stages of the testes by month. Only data from specimens larger than the minimum size at sexual maturity for males (TL=325 mm) have been used in this table. Stage 2 = early spermatogenesis; stage 3 = late spermatogenesis; stage 4 = mature.

	Maturity stage of the testes		
Month	2	3	4
Jan	22	5	12
Feb	40	14	7
Mar	1	4	17
Apr	3	3	5
May	4	24	18
Jun			3
Jul		2	3
Sep		1	3
Oct		8	15
Nov			14
Dec		2	17

Table 5

Number of female *Lophius litulon* in the East China and Yellow seas at the various maturity stages of the ovaries by month. Only data from specimens larger than the minimum size at sexual maturity for females (TL=546 mm) have been used in this table. Stage 1 = immature; stage 2 = developing; stage 3 = mature; stage 4 = spawning; stage 5 = spent; stage 6 = resting.

	Maturity stage of the ovary						
Month	1	2 (early)	2 (late)	3	4	5	6
Jan		5					
Feb	1	8	4		1		
Mar		3	4	1	4	4	
Apr			2	3	1	3	
May					1	3	2
Jun						1	1
Jul	1						2
Aug	1						
Sep	3						
Nov	3	3					
Dec		5					

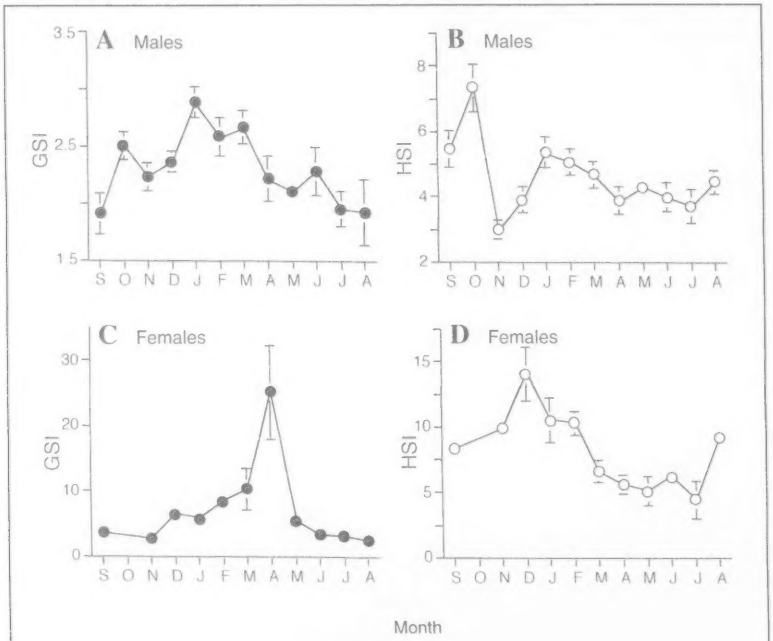

Figure 8

Monthly changes in the mean gonadosomatic index (GSI) and hepatosomatic index (HSI) for mature male (n=306) and female (n=67) *Lophius litulon* in the East China and Yellow seas. Only specimens larger than the size at 50% sexual maturity for males (L_{50}=362 mm) and females (L_{50}=567 mm) were used in our study. Vertical lines indicate standard error.

Discussion

The testicular structure of *L. litulon* is similar to that of other teleosts with unrestricted spermatogonial (Grier et al., 1980; Grier, 1981) or lobular type testes (Billard et al., 1982; Billard, 1986). Although the process of spermatogenesis conformed to that of other teleosts, it was not completed within the germinal cysts. Rather, spermatids were released into the lumina of the seminiferous tubules and did not differentiate synchronously. This form of spermatogenesis first described in *Lepadogaster lepadogaster* (Mattei and Mattei, 1978), and later termed "semi-cystic" type (Mattei et al., 1993), has subsequently been reported in Neoceratiidae (Jespersen, 1984), blennioid fishes (Lahnsteiner and Patzner, 1990), *Ophidion* sp. (Mattei et al., 1993), *Opistognathus whitehurstii* (Manni and Rasotto, 1997), and *L. setigerus* (Yoneda et al., 1998c).

The ovarian structure of *L. litulon* is similar to that reported in other Lophiiformes such as *L. piscatorius* (Afonso-Dias and Hislop, 1996), *Antennarius scaber*, *Histrio histrio*, and *Ogcocephalus vespertilio* (Rasquin, 1958), *L. americanus* (Armstrong et al., 1992), and *L. setigerus* (Yoneda et al., 1998a). Most female Lophiiformes are thought to spawn gelatinous egg masses, within which individual eggs float in separate chambers (Rasquin, 1958; Armstrong et al., 1992; Afonso-Dias and Hislop, 1996; Yoneda et al., 1998a, 1998c). In *L. litulon*, as in other lophiiform fishes (Rasquin, 1958; Armstrong et al., 1992; Yoneda et al., 1998a, 1998c), gelatinous material was secreted from the epithelium of both the ovigerous lamellae and the ovarian wall. Rasquin (1958) compared the structure of the ovary of *H. histrio* with that of the released egg mass and concluded that the shape of the egg mass was a replica of the internal surface of the ovary. This is expected to be the case in other fishes of the family Lophiiformes. Each stalk-like ovigerous lamella is thought to serve as a "mold," forming a separate chamber within the gelatinous egg mass. The arrangement of oocytes, with the most advanced oocytes at the margins of the ovigerous lamellae, may facilitate the release of mature oocytes into each chamber.

Our examination of the gonadal condition of both sexes indicates that *L. litulon* spawns during the period from February through May. Most females with late-developing, mature, or spawning ovaries are found in March and April. This finding agrees with previous reports. The peak of the spawning season of *L. litulon* occurred between February and March in inshore waters off Kyushu Island (Mito, 1963) and in March and April in the East China and Yellow seas (Yamada, 1986). In Sendai Bay, off the northeast coast of Honshu Island, Japan, the spawning season of *L. litulon* occurs between May and July (Kosaka, 1966).

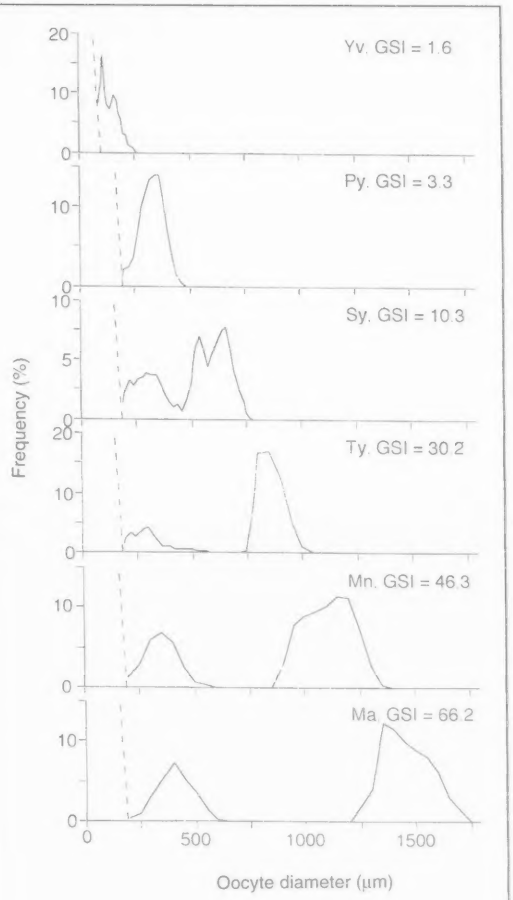

Figure 9

Size-frequency distribution of oocytes at the different stages of maturation in the ovaries of *Lophius litulon*. All oocytes ≥100 μm diameter were measured in yolk vesicle stage ovaries, whereas at all other ovarian stages only oocytes ≥200 μm were measured. GSI = gonadosomatic index; Yv = yolk vesicle stage; Py = primary yolk stage; Sy = secondary yolk stage; Ty = tertiary yolk stage; Mn = migratory nucleus stage; Ma = mature stage.

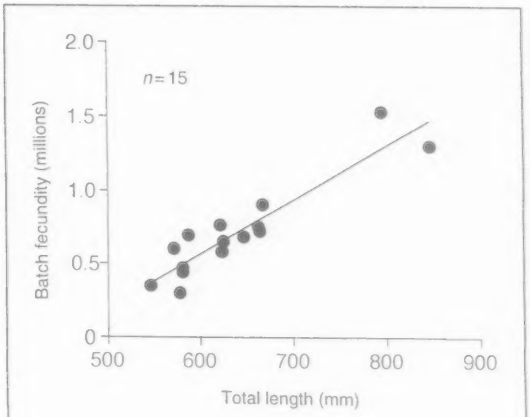

Figure 10

Relationship between batch fecundity and total length for *Lophius litulon*. Females (n=15) with secondary yolk stage ovaries were collected from December through February. $BF = (-1.64 \times 10^6) + 3688.13\ TL$ ($546 \leq TL \leq 846$).

Table 6

Gonadosomatic index (GSI, mean ± SE) and hepatosomatic index (HSI, mean ± SE) at each stage of maturity for male and female *Lophius litulon*. Values with different superscripts are significantly different (Dunn's multiple comparison test, $P<0.05$). See tables 5 and 6 for definitions of maturity stages.

Maturity stage of the gonads	n	GSI	HSI
Male			
1	47	1.17 ±0.25^a	5.57 ±0.77
2	143	2.00 ±0.22^a	4.70 ±0.44
3	63	2.09 ±0.10^a	4.80 ±0.37
4	114	2.48 ±0.07^b	4.50 ±0.24
Female			
1	206	1.34 ±0.08^a	5.40 ±0.25^a
2 (early)	24	5.73 ±0.42^b	10.38 ±0.70^b
2 (late)	10	15.27 ±2.02^b	11.21 ±1.30^b
3	4	51.78 ±5.49^b	3.58 ±0.23^a
4	7	7.07 ±0.39^b	6.03 ±0.84^{ab}
5	11	6.58 ±0.61^b	4.34 ±0.53^a
6	5	2.85 ±0.37^a	6.37 ±0.94^{ab}

This difference in spawning season depending on latitude would indicate that the spawning season of *L. litulon* in Japanese waters occurs progressively later, with increasing latitude. This also occurs with *L. americanus* (Bigelow and Schroeder, 1953) in American waters and with *L. piscatorius* (Afonso-Dias and Hislop, 1996) in northern European waters.

After spawning, ovaries in two conditions (stages 4 and 5) were observed during our study. Females had postovulatory follicles and yolked oocytes at the primary or secondary yolk oocyte stages. Secondary yolk stage oocytes were more often present in the ovaries of females collected in the first half of the spawning period (February–March). It seems likely that these normally develop into yolked oocytes because no signs of oocyte atresia were observed in histological examination. Specimens with primary yolk oocytes were collected between March and May. However, there was evidence of atresia in half of the fish collected during the latter half of the spawning period (April–May).

A solitary female *L. litulon*, in Oarai Aquarium, released an infertile egg mass on 19 April 1994 and 35 days later extruded another mass.[2] Similarly, another captive female spawned three times, on 15 February, 2 June, and 21 July 1998. These data indicate that *L. litulon* may have the potential to spawn more than once a year, although the five spawnings observed in the aquarium were not accompanied by normal spawning behavior. Recently, we reported a case of repeated spawning in *L. setigerus,* which has a long spawning period from May to November (Yoneda et al., 1998a). In contrast, *L. americanus* (Feinberg, 1984) and *L. piscatorius* (Afonso-Dias and Hislop, 1996) are believed to spawn only once a season. Future field studies are required to determine the spawning frequency for *L. litulon*, which will be important for estimating its reproductive potential.

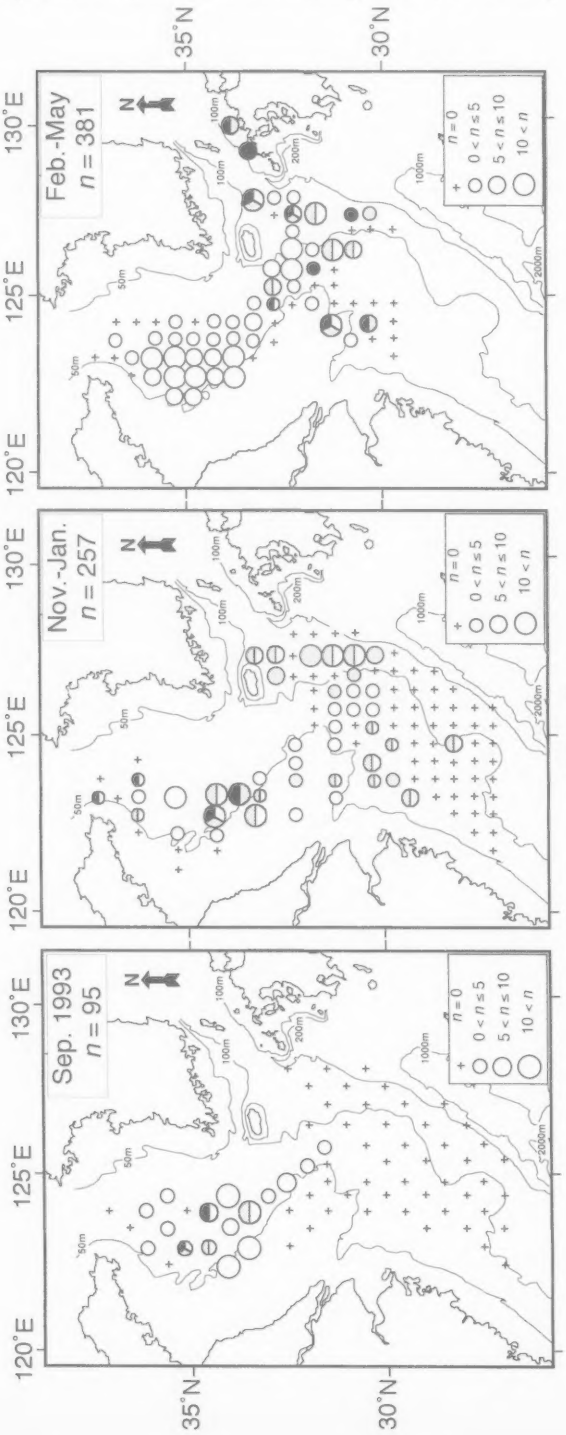

Figure 11

Geographical distribution of specimens of *Lophius litulon* collected in the East China and Yellow seas at three different times of the year. Specimens were identified as sexually immature individuals (open area), sexually mature males (stippled area) and females (solid area). Sexually mature individuals were defined as fish collected in September and November–January, larger than the size at 50% sexual maturity (male=362 mm TL, female=567 mm TL) or fish caught in February–May with stage 4 testes or ovaries that had matured to a least the late-2 (tertiary yolk stage of oocyte) stage. *n* = number of fish examined.

Both sexes of *L. americanus* inhabiting northern waters were larger and a little younger at 50% sexual maturity than fish from more southern waters (Almeida et al., 1995). In *L. litulon,* there also appears to be a size difference at sexual maturity between fish from the East China and Yellow seas (our study) and those from Sendai Bay off northeast Honshu Island (Kosaka, 1966); the minimum size at sexual maturity for males and females was 340 mm body length (BL) and 600 mm BL for Kosaka's report and 325 mm TL and 546 mm TL for our results, respectively. The study from Sendai Bay, however, was carried out about 30 years ago and did not identify the age at sexual maturity; therefore the differences by area for size at sexual maturity may be attributed to different sampling times of the year or to different growth rates. In the East China and Yellow seas, females *L. litulon* reached sexual maturity at larger than 500 mm BL, and the minimum size at sexual maturity was about 350 mm BL in male, as previously reported by Yamada (1986). The size at sexual maturity for female *L. litulon* in the 1980s (Yamada, 1986) is fairly close to our results, whereas that for males is higher than that found in our study. Although the reason for the size difference found in males at sexual maturity is unclear, it may be due to a difference in criteria for maturity. Our histological criteria for maturity in males were based on the characteristics of testicular development with unique spermatogenesis; therefore our determination of sexual maturity is more reliable than macroscopic methods.

There was a noticeable inverse correlation between the development of the ovary and the weight of the liver (HSI). The de-

[2] Kofuji, K. 1998. Personal commun. Oarai Aquarium, Isohama, Oarai, Higashi-Ibaraki, Ibaraki 311-1301, Japan.

crease in HSI that is associated with increasing GSI is probably due to materials that have been stored in the liver becoming mobile and being transferred to the gonads. In teleosts, as in most other vertebrates, the precursor protein of yolk (vitellogenin) is synthesized in the liver. The secreted vitellogenin is selectively removed from the bloodstream by the developing oocytes (Wallace and Selman, 1981; Nagahama, 1987). The rapid accumulation of yolk probably accounts for the decrease in the weight of the liver.

In many fish, batch fecundity is estimated by using migratory nuclei or hydrated oocytes, which can be easily distinguished from the less advanced oocytes: e.g. *Engraulis mordax* (Hunter and Goldberg, 1980; Hunter et al., 1985), *Thunnus albacares* (Schaefer, 1996), and *Rhombosolites aurorubens* (Cuellar et al., 1996). We found that during and after the tertiary yolk stage, a large amount of gelatinous material was rapidly secreted and accumulated in the ovarian lumen. Hence, counts of advanced oocytes from a small portion of the ovary, when extrapolated to the total weight of the gelatinous material, may give more variable estimates. These findings were also evident in *L. setigerus* (Yoneda et al., 1998a). However, the oocyte size-frequency profiles indicated that when the most advanced oocytes reached the secondary yolk stage, they formed a batch that was almost completely separated from the adjacent group of smaller oocytes. These ovarian characteristics of *L. litulon* imply that estimates of batch fecundity can be made only by using oocytes that have attained the secondary yolk stage.

Both the immature and mature distribution of *L. litulon* ranged into the East China and Yellow seas, as previously reported by Yamada (1986) and Tokimura.[1] This species is caught mainly at depths between 50 and 100 m and at temperatures ranging from 6 to 13°C (Yamada, 1986; Tokimura[1]). In the Yellow Sea, the Yellow Sea Central Cold Water, cooler than 10°C, is found throughout the year and there are few seasonal changes in water temperature (±2–3°C). The water of the East China Sea remains lower than 13°C owing to the influence of the Continental Coastal Cold Water in the winter and spring, whereas in summer it increases higher than 20°C (Kondo, 1985; Tokimura[1]). These oceanographic conditions in the East China and Yellow seas may influence the migration of *L. litulon* from area to area throughout the year. A seasonal movement of *L. litulon* has also been reported in Sendai Bay (Kosaka, 1966; Omori, 1979). *Lophius litulon* are most abundant in shallow waters between February and June. From August through October, they disperse toward deeper waters. This seasonal movement in Sendai Bay is observed mainly in immature fish and is thought to be associated with their feeding activities (Kosaka, 1966). In *L. americanus*, a seasonal migration, thought to occur in response to changes in hydrographic conditions, has been observed along the northeastern coast of the United States (Jean, 1965; Almeida et al., 1995).

During the February–May spawning season, mature males and females with ovaries in a condition that suggests they are either about to spawn, or have just spawned, are found in the East China Sea and the coastal waters off Kyushu. In contrast, immature individuals were distributed throughout the East China and Yellow seas during this same period. This indicates that the spawning grounds of *L. litulon* cover a large area, extending from the East China Sea to inshore waters off Kyushu. Furthermore, our study reveals the migratory pattern of both sexes of *L. litulon* in relation to the spawning grounds in the period before the spawning season. In February, with the onset of the spawning season, females collected in the northern East China Sea had developing ovaries (secondary or tertiary yolk stage), whereas those collected in the Yellow Sea had immature or primary yolk stage ovaries. This finding implies that the start of the migration of females seems to be more dependent on ovarian development than oceanographic conditions. Different migratory patterns of the two sexes before spawning have also been reported in European plaice, *Pleuronectes platessa*, in the Straits of Dover off England (Arnold and Metcalfe, 1995). Our study has identified the spawning grounds and migratory pattern of *L. litulon* in broad terms. Further research is needed to identify specific spawning grounds and details of the migratory behavior of this species.

Acknowledgments

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Differential parasitism by *Naobranchia occidentalis* (Copepoda: Naobranchiidae) and *Nectobrachia indivisa* (Copepoda: Lernaeopodidae) on northern rock sole (*Lepidopsetta polyxystra* Orr and Matarese, 2000) and southern rock sole (*L. bilineata* Ayres, 1855) in Alaskan waters

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Abstract–Northern rock sole (*Lepidopsetta polyxystra* Orr and Matarese, 2000) and southern rock sole (*L. bilineata* Ayres, 1855) from the Gulf of Alaska and northern rock sole from the Aleutian Islands were examined for gill parasites. Four species of copepod parasites were identified: *Naobranchia occidentalis* and *Nectobrachia indivisa* were the most common. Both parasites were more prevalent on northern rock sole (22% and 15%, respectively) than on southern rock sole (5% and 1%, respectively) in the Gulf of Alaska samples. Northern rock sole tended to have a greater mean intensity of *Naobranchia occidentalis* than southern rock sole but there was not a significant difference because of the high variance about the means; too few southern rock sole were infested by *Nectobrachia indivisa* for comparison. Northern rock sole from the Aleutian Islands region had a significantly greater prevalence (36%) and mean intensity (10.2/infested fish) of *Naobranchia occidentalis* than northern rock sole from the Gulf of Alaska (22%, and 4.4, respectively) but did not differ significantly in prevalence and mean intensity of *Nectobrachia indivisa*. Parasitized male northern rock sole from the Gulf of Alaska had a significantly reduced weight at length, indicating a possible effect of parasitism. *Naobranchia occidentalis* selectively infested larger northern rock sole and only the largest southern rock sole. *Nectobrachia indivisa* also were found on larger northern rock sole but did not infest enough southern rock sole to describe a trend. Southern rock sole males were not infested by either parasite. *Naobranchia occidentalis* preferred to infest the middle gill arches of hosts and *Nectobrachia indivisa* preferred to infest the exterior gill arches of hosts.

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The rock soles (*Lepidopsetta* spp.) are important commercial flatfish species that inhabit the continental shelf of the north Pacific Ocean (Hart, 1973). Stock assessment bottom trawl surveys conducted by the Alaska Fisheries Science Center (AFSC) historically recognized only one species of rock sole occurring in four survey areas: eastern Bering Sea, Aleutian Islands, Gulf of Alaska, and western U.S. coast. Recent larval morphometrics by Matarese et al. (1989) and a generic revision by Orr and Matarese (2000) have demonstrated that there are actually two species of rock sole that overlap in the AFSC survey areas. The northern rock sole (*L. polyxystra* Orr and Matarese, 2000) ranges throughout the Bering Sea and Aleutian Islands to Puget Sound, whereas the southern rock sole (*L. bilineata* Ayres, 1855) ranges from the Islands of Four Mountains in the eastern Aleutian Islands to Mexico (Orr and Matarese, 2000). With the knowledge of this recent research, field biologists began separating the two rock sole species in AFSC bottom trawl surveys starting in 1996. The northern rock sole is distinguished by higher gill-raker counts and a whiter blind side than southern rock sole occurring in the same trawl hauls (Orr and Matarese, 2000).

While examining gill rakers to identify specimens of rock soles captured near the Shumagin Islands during the 1996 Gulf of Alaska survey, we noticed that several live, apparently healthy, northern rock soles had pink or white gill filaments, a condition normally associated with dead fish. On close examination, we found small copepod parasites attached to the gill filaments of these fish. Southern rock soles from the same trawl hauls usually had red, apparently healthy gill filaments and were less frequently parasitized. Therefore we surveyed northern and southern rock soles in selected hauls from the Gulf of Alaska in 1996 for the presence of these parasites and saved infested heads for parasite identification and enumeration in the laboratory. In 1997, we conducted the same parasite investigation in several hauls in the Aleutian Islands region. Our main objective was to quantify differences in the prevalence (percent fish infested) and mean intensity (average number of parasites per infested fish) of gill parasites infesting the northern and southern rock soles (see Margolis et al., 1982; Bush et al., 1997, for complete definitions of ecological terms in parasitology). Secondary objectives were to test for regional differences in prevalence and mean intensity, to describe and compare site preferences of the parasites, and to determine if parasites influenced weight at length for parasitized fish.

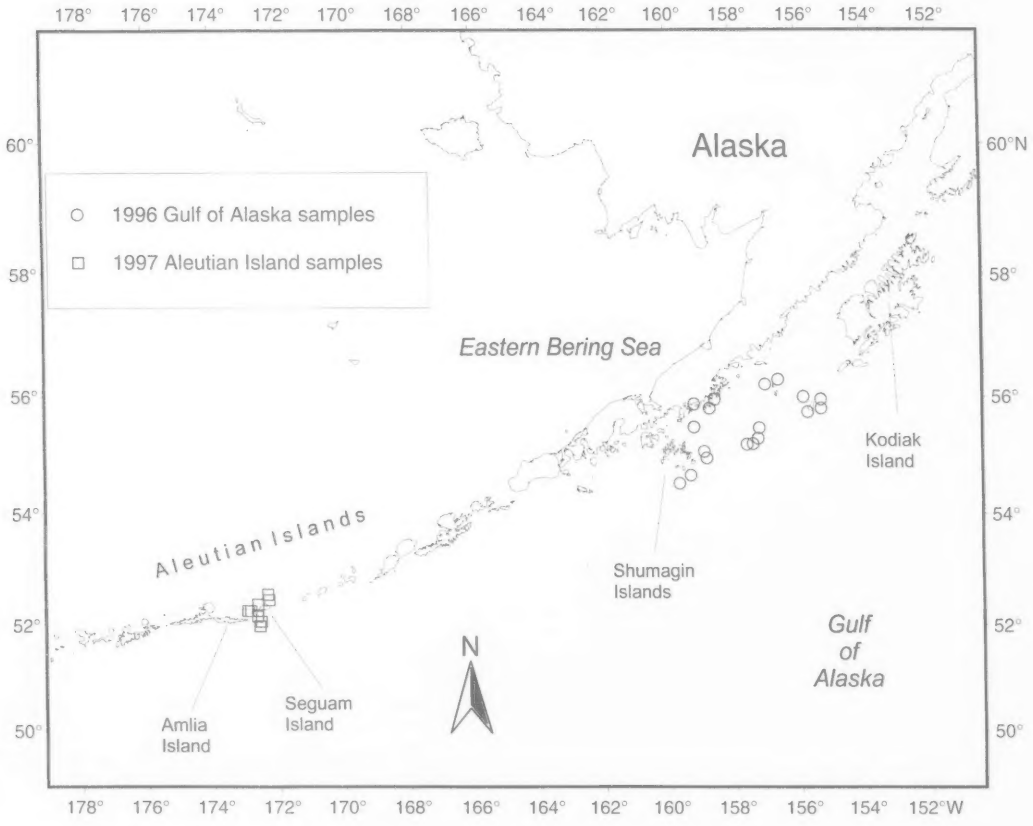

Figure 1

Location of trawl hauls in the Gulf of Alaska and Aleutian Islands where northern and southern rock sole were examined for gill parasites.

Materials and methods

Between 8 and 18 June 1996 (Table 1), northern and southern rock soles captured in a series of trawl hauls from the western Gulf of Alaska were examined for parasites (Fig. 1). Between 25 and 27 June 1997 (Table 1), we examined northern rock soles from a series of trawl hauls around Seguam Island and the east end of Amlia Island in the central Aleutian Islands. The two sampling areas are approximately 850 km apart. We scanned the interior and exterior surfaces of gill filaments on all gill arches for parasites. All rock soles were examined in hauls with few fish ($n \leq 50$), and a random selection of fish in larger hauls were subsampled in a manner similar to that used for obtaining a random subsample for lengths (see Martin, 1997, for Gulf of Alaska bottom trawl survey methods). For each parasitized fish, we measured the fork length (FL) in centimeters, weight (±2 grams), determined the sex, and removed and froze the entire head, including gill arches, at sea. Lengths and weights were also collected from uninfested northern and southern rock soles in the Gulf of Alaska survey for comparisons with parasitized fish.

Frozen heads were thawed slowly in a refrigerator; thawing heads quickly in warm water produced gill filaments with an excess of mucus, making it difficult to locate parasites. Host species identification was confirmed by examining the gill rakers on the first gill arch on the blind side, and by counting supraorbital pores (Orr and Matarese, 2000). The internal and external surfaces of all gill filaments were examined for parasites with a dissecting microscope. The parasites were removed from gill filaments by washing with water into a filter, or pulling with tweezers, or by removing the gill filament if the parasite was well-anchored. All parasites were preserved in 10% formalin for 3–5 days and stored in 70% ethanol with a small amount of glycerol (Kabata and Cousens, 1972). Fish heads were fixed in 10% formalin for up to one week and stored in 70% ethanol.

We identified the parasites by using the key of Kabata (1988), and Kabata verified our identifications. Generally, only female parasites, which measured at least 2 millimeters in length, were enumerated. Males were found occasionally, sometimes attached to females. However, males were too small (<0.3 mm in length) to identify and quantify; therefore males were not included in any summaries or

Table 1

Summary of field collection information for northern and southern rock sole from the two sampling areas of the western Gulf of Alaska and the central Aleutian Islands.

Area	Dates	Hauls	Depth range (m)	Temperature range (Celcius)
Gulf of Alaska	8 to 18 Jun 1996	18	46–149	4.0–7.4
Aleutian Islands	25 to 27 Jun 1997	8	143–232	3.9–4.5

Table 2

Summary of fish examined at sea and parasite collections. Mean intensity = average number of parasites for each infested fish. Range is from minimum to maximum numbers of parasites for each infested fish.

Area and rock sole species	Fish examined at sea for gill parasites	Fish infested with either gill parasite	*Naobranchia occidentalis*			*Nectobrachia indivisa*		
			Prevalence (%)	Mean intensity	Range	Prevalence (%)	Mean intensity	Range
Gulf of Alaska								
Northern	225	58	22	4.4	1–22	15	3.8	1–21
Southern	282	15	5	2.9	1–13	1	2.0	1–3
Aleutian Islands								
Northern	237	89	36	10.2	1–45	9	3.1	1–8

analyses. Differences in parasite prevalence between the northern and the southern rock sole were determined with chi-square tests, and differences in mean intensity were determined with Welch's approximate *t*-test (Zar, 1984).

To test for significant differences in the length-weight relationship between parasitized (containing *Naobranchia occidentalis* or *Nectobrachia indivisa*, or both) and unparasitized fish, natural log-transformed length and weight data were compared by linear regression. The slopes and *Y*-intercepts were compared by using *F*-ratios.

Results

Parasite species

Four species of copepod parasites were identified from the gills of the infested fish. The most common parasite was *Naobranchia occidentalis* Wilson, 1915, which attaches to the gill filaments by its modified second maxillae (Kabata, 1988). This parasite was easily removed in the laboratory; freezing and thawing the specimens may, therefore, have loosened the parasite's grip. The next most common parasite, *Nectobrachia indivisa* Fraser, 1920, firmly anchors in the filament and could only be removed by cutting the filament or breaking off the bulla. *Nectobrachia indivisa* was almost always found attached to the tips of the gill filaments. Two specimens of *Acanthochondria vancouverensis* were found unattached in the gill chambers of two Gulf of Alaska northern rock sole, constituting the first record of parasitism in wild rock sole for this species (Kabata[1]). A single specimen of *Haemobaphes diceraus* was found attached on the third gill arch, eyed side, of a Gulf of Alaska northern rock sole (Kabata[2]). Kabata (1988) reported that all of these parasites occur on rock sole, except for *A. vancouverensis*. Small, highly mobile leeches were also frequently noted on the gills of fish caught in the Gulf of Alaska survey, but because of their mobility, their presence could not be reliably documented. We did not attempt to enumerate or identify this species.

Gulf of Alaska A total of 225 northern and 282 southern rock soles were visually examined for parasites at sea during the 1996 Gulf of Alaska survey, and 78 rock sole heads were collected because they appeared to have at least one copepod gill parasite (Table 2). *Naobranchia occidentalis* or *Nectobrachia indivisa* (or both) were found on 73 of the collected heads during laboratory dissection (58 northern and 15 southern rock sole). Only one juvenile female or

[1] Kabata, Z. 1998. Personal commun. Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, Canada, V9R 5K6. Kabata suggested that we consider this incidence of parasitism by *A. vancouverensis* to be the first record of parasitism in wild rock sole by this species. A former record of parasitism by this species was for aquarium fish only.

[2] Kabata, Z. 1998. Personal Commun. Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, Canada, V9R 5K6. Kabata confirmed our tentative identification of *Haemobaphes* and identified it with fair certainty as *H. diceraus*.

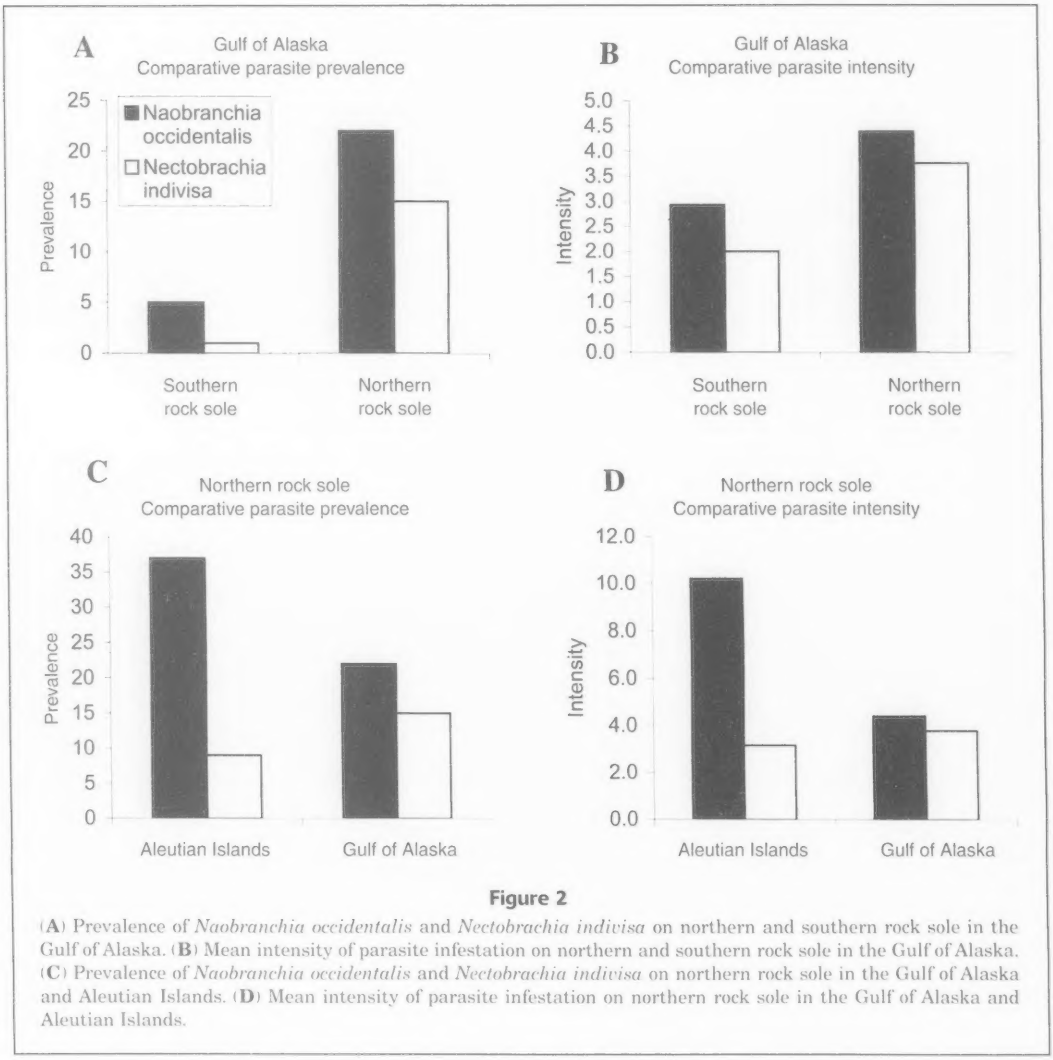

Figure 2

(**A**) Prevalence of *Naobranchia occidentalis* and *Nectobrachia indivisa* on northern and southern rock sole in the Gulf of Alaska. (**B**) Mean intensity of parasite infestation on northern and southern rock sole in the Gulf of Alaska. (**C**) Prevalence of *Naobranchia occidentalis* and *Nectobrachia indivisa* on northern rock sole in the Gulf of Alaska and Aleutian Islands. (**D**) Mean intensity of parasite infestation on northern rock sole in the Gulf of Alaska and Aleutian Islands.

postreproductive adult *Naobranchia occidentalis* was found in the Gulf of Alaska samples. The original at-sea identification of the two rock sole species was confirmed for all but one fish in the laboratory (a northern rock sole was incorrectly identified at sea as a southern rock sole).

Both *Naobranchia occidentalis* and *Nectobrachia indivisa* were more prevalent (chi square test, α=0.05, P<0.001) on the northern rock sole (22% and 15% of the 225 fish examined, respectively) than on the southern rock sole (5% and 1% of the 282 fish examined, respectively, Fig. 2A). Mean intensity was not significantly different between the northern (4.4/fish, range 1–22) and southern rock sole (2.9/fish, range 1–13) for *Naobranchia occidentalis* (Welch's approximate t-test, α=0.05, df=28, P=0.08, Fig. 2B) owing to a single southern rock sole with 13 parasites. Mean intensity also was not significantly different between the northern and the southern rock sole for *Nectobrachia indivisa* (Welch's approximate t-test, α=0.05, df=2, P>0.05); however only two southern rock soles were infested with *N. indivisa*. A chi-square test showed that infestation of northern rock sole by *N. indivisa* was not independent of infestation by *Naobranchia occidentalis* (α=0.05, P<0.001). Thus, northern rock sole infested by one species of parasite had an increased likelihood of also being infested by the other. However, infestation of southern rock sole by *Nectobrachia indivisa* was independent of infestation by *Naobranchia occidentalis* (P>0.05).

Aleutian Islands Only northern rock soles were identified at sea in sampled hauls from the Aleutian Islands region, and laboratory analysis confirmed their species identification. A total of 237 northern rock soles from 8 trawl hauls was examined at sea for gill parasites: 90 fish appeared to have at least one gill parasite and their heads were frozen

at sea (Table 2). None of the fish had abnormally pale gill filaments. *Naobranchia occidentalis* or *Nectobrachia indivisa* (or both) were found on all but one of the northern rock soles examined in the laboratory. No other parasite species were observed. Approximately 17% of the *Naobranchia occidentalis* were juvenile females. Northern rock soles infested by one species of parasite had an increased likelihood of also being infested by the other species of parasite (chi square test, α=0.05, P<0.001), similar to our observations for northern rock soles from the Gulf of Alaska.

Area and species infestation comparisons

Naobranchia occidentalis was more prevalent (chi square test, α=0.05, P<0.01) on the northern rock soles in the Aleutian Islands (36%) than on fish from the Gulf of Alaska (22%) (Fig. 2C). The northern rock soles from the Aleutian Islands also had a significantly higher mean intensity of *N. occidentalis* (Welch's approximate t-test, α=0.05, df=127, P<0.001; 10.2/fish) than northern rock soles from the Gulf of Alaska (4.4/fish, Fig. 2D). There were no differences in either prevalence (chi-square test, α=0.05, P >0.05) or mean intensity (Welch's approximate t-test, α=0.05, df=50, P>0.05) of *Nectobrachia indivisa* on the northern rock soles from the Aleutian Islands and Gulf of Alaska.

Trends in parasite infestations—arches and sides

Heads of fish from the 1996 Gulf of Alaska survey had been frozen for a year before examination and the gill filaments were in poor condition. As a result, only a small percentage of *Naobranchia occidentalis* were still attached to a gill arch, and it was not possible to detect preferences of *N. occidentalis* for individual gill arches, or for eyed-side or blind-side arches, on northern rock sole (Table 3). Ninety-one percent of the observed *Nectobrachia indivisa* were still firmly anchored in the gill filaments on northern rock sole, were evenly distributed per side (60), and showed a preference for the outer arches over the inner arches on both sides of the fish (Table 3). All *Naobranchia occidentalis* on the southern rock sole from the Gulf of Alaska were unattached. Four *Nectobrachia indivisa* were found still attached on the blind side of southern rock sole from the Gulf of Alaska, but this small sample was insufficient for analysis.

Aleutian Islands samples were frozen for only a few weeks prior to examination in the laboratory and were in much better condition than samples from the Gulf of Alaska survey. The infested gill arch was determined for 83% of the *Naobranchia occidentalis* and for 97% of the *Nectobrachia indivisa* (Table 3). For northern rock sole from the Aleutian Islands, the total number of *Naobranchia occidentalis* was higher on the blind side (452) than the eyed side (414) and equal on both sides for *Nectobrachia indivisa* (33); these results nearly duplicated those observed for northern rock sole from the Gulf of Alaska. *Naobranchia occidentalis* showed a strong preference for the middle and inner gill arches on both eyed and blind sides (Table 3). The results were mixed for *Nectobrachia indivisa*; parasites on the blind side showed a preference for the outer arches, whereas parasites on the eyed side showed

Table 3

Counts of female parasites by gill arch attachment (1st=exterior arch, 4th=interior arch). Unattached parasites (U.) were on or in the area of the eyed-side or blind-side gill arches. Loose parasites were not associated with either set of gill arches. Male parasites were too small to be reliably enumerated and are not included in this summary. Juvenile female parasites are included in the totals and are also listed separately.

Area and rock sole species	Parasite species	Eyed side gill arches						Blind side gill arches						Grand total	Juvenile
		1st	2nd	3rd	4th	U.	Subtotal	1st	2nd	3rd	4th	U.	Subtotal	Loose		
Gulf of Alaska																
Northern	*Naobranchia occidentalis*	0	0	1	0	99	100	0	0	3	0	106	109	6	215	1
	Nectobrachia indivisa	23	16	16	1	4	60	26	14	12	5	3	60	4	124	0
Southern	*Naobranchia occidentalis*	0	0	0	0	11	11	0	0	0	0	30	30	0	41	0
	Nectobrachia indivisa	0	0	0	0	0	0	3	0	1	0	0	4	0	4	0
Aleutian Islands																
Northern	*Naobranchia occidentalis*	27	119	139	62	67	414	22	97	181	73	79	452	2	868	146
	Nectobrachia indivisa	5	10	12	5	1	33	15	8	5	4	1	33	0	66	0

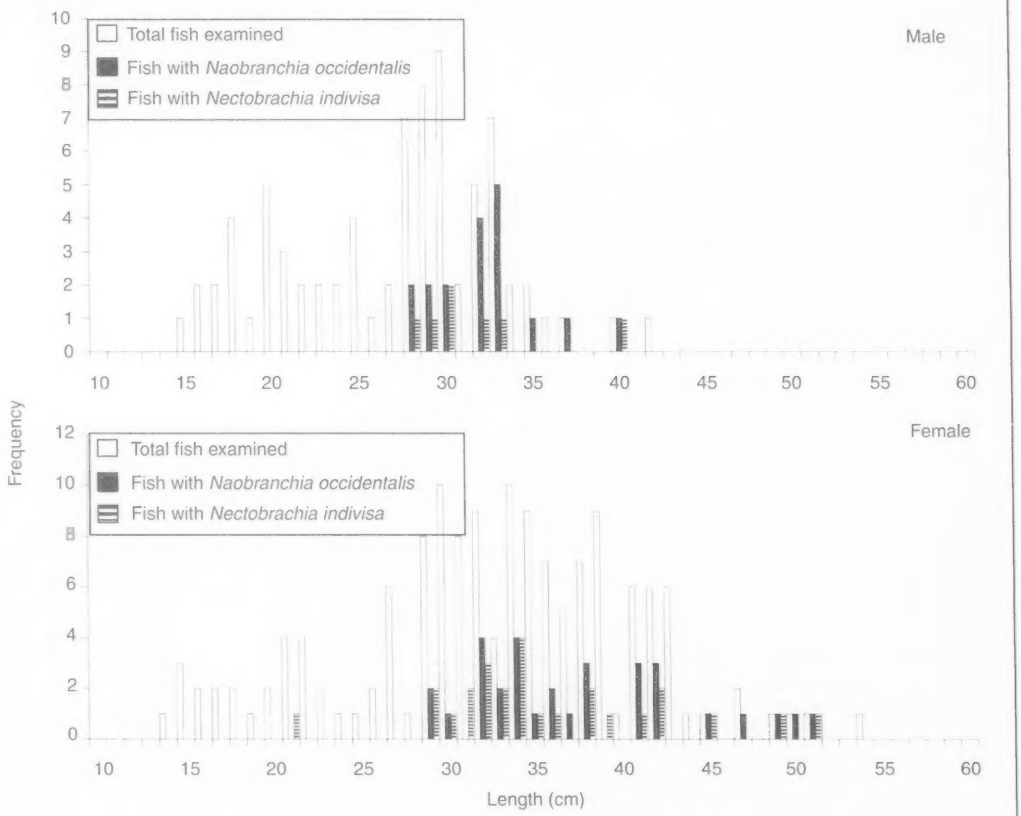

Figure 3

Length frequency of male and female northern rock sole examined for parasites from the Gulf of Alaska. Numbers of fish infested with one parasite species added to those infested with the other parasite species may exceed the total because several fish were infested with both parasite species.

a preference for middle gill arches, and overall, there was a slight preference for outer arches (Table 3). Although there were numerous juvenile *Naobranchia occidentalis* parasites on northern rock soles from the Aleutian Islands, their individual positions were not recorded separately from the adults.

Trends in parasite infestations—species, sex, and size

Gulf of Alaska A wide size range of northern rock sole males (15–42 cm FL) and females (14–54 cm FL) were examined for parasites during the Gulf of Alaska survey (Fig. 3), but *Naobranchia occidentalis* was found only on larger males (28–40 cm FL) and females (29–51 cm FL). Similarly, *Nectobrachia indivisa* was found only on larger males (28–40 cm FL) and females (29–51 cm FL), with the exception of a single, small (21 cm FL) infested female.

None of the male southern rock soles (19–40 cm FL) were infested with either parasite species, but male southern rock soles were uncommon in our survey catches and only 28 fish were examined (Fig. 4). A total of 254 female southern rock soles (14–58 cm FL) were examined for parasites during the survey and *Naobranchia occidentalis* infested only 14 of the larger females (42–52 cm FL). Only two relatively large (37 and 47 cm FL) female southern rock soles were infested with *Nectobrachia indivisa*.

Aleutian Islands Male (19–37 cm FL) and female (20–46 cm FL) northern rock soles from the Aleutian Islands were examined, and *Naobranchia occidentalis* was found only in larger individuals (24–37 cm FL males and 28–44 cm FL females, Fig. 5). The size range of fish infested with *Nectobrachia indivisa* was slightly more restricted (24–33 cm FL males and 28–43 cm FL females) than the size range of fish infested with *Naobranchia occidentalis*.

Length-weight relationships

Parasitized (range 28–40 cm FL) and unparasitized (range 18–36 cm FL) male northern rock soles from the Gulf of

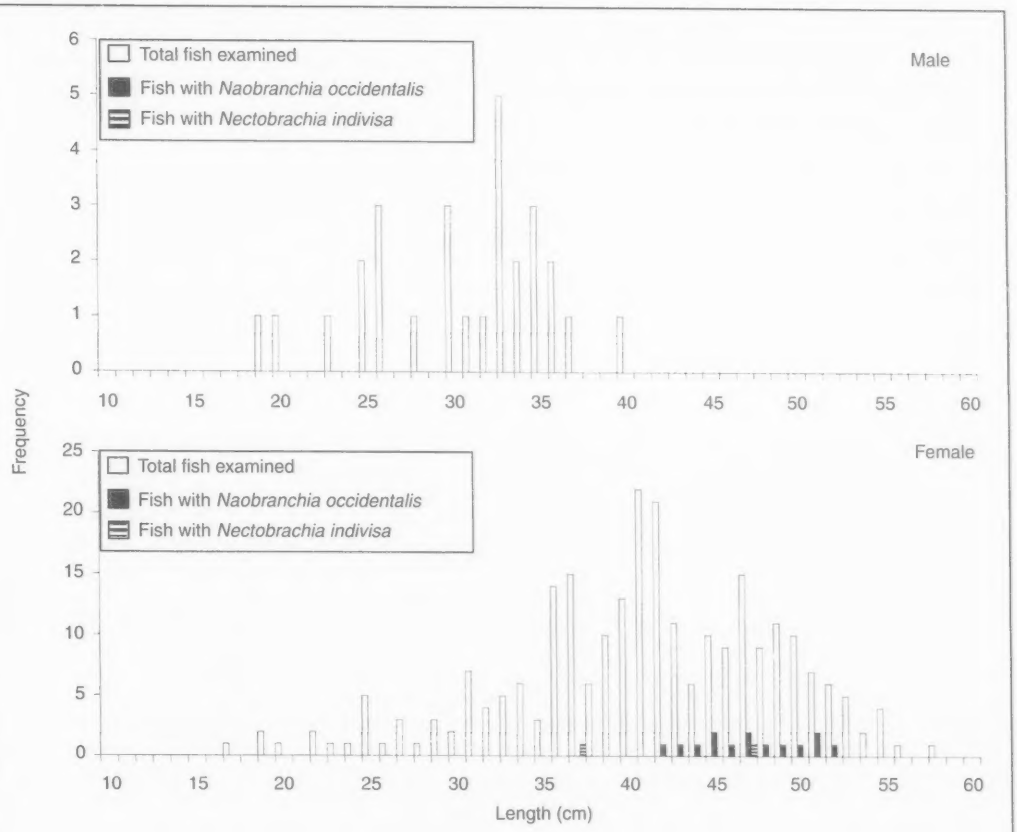

Figure 4

Length frequency of male and female southern rock sole examined for parasites from the Gulf of Alaska. Numbers of fish infested with one parasite species added to those infested with the other parasite species may exceed the total because several fish were infested with both parasite species.

Alaska did not have significantly different length-weight slopes (df=1, F-ratio=0.29, $P>0.05$) but had significantly different intercepts (df=1, F-ratio=13.74, $P<0.001$). For example, a 33-cm-FL parasitized male northern rock sole from the Gulf of Alaska had an estimated weight of 407.5 grams, whereas an unparasitized fish of the same length weighed an estimated 451.4 grams, a difference of more than 10%. The length-weight slopes and intercepts were not significantly different for female northern or southern rock soles from the Gulf of Alaska. No comparison could be made between parasitized and unparasitized Aleutian Islands fish because individual weights were not taken for unparasitized fish.

Discussion

Laboratory examination confirmed our original observations that copepod parasites were more prevalent on the northern rock soles from the Gulf of Alaska than on southern rock soles. There could also be a higher mean intensity for both species of parasites on the northern rock sole, but our analysis was limited by a small sample size and high variability within the sample. Of the two gill parasites examined in detail, *Naobranchia occidentalis* was more prevalent and caused more intense infestations than did *Nectobrachia indivisa*. Our sampling efforts in the Aleutian Islands occurred beyond the geographic range of southern rock sole and indicated that the northern rock sole had a higher prevalence and greater mean intensity of *Naobranchia occidentalis* than the northern rock sole in the Gulf of Alaska. Differences in parasite prevalence and mean intensity between the Gulf of Alaska and Aleutian Island samples were confounded by sampling in different years, limited areal coverage, limited temperature range, and greater depths in the Aleutian samples. Also, the significance of the large number of juvenile *N. occidentalis* in the Aleutian Island samples is not known. Despite these limitations, it is noteworthy that none of the northern rock soles heavily infested with *Naobranchia occidentalis*

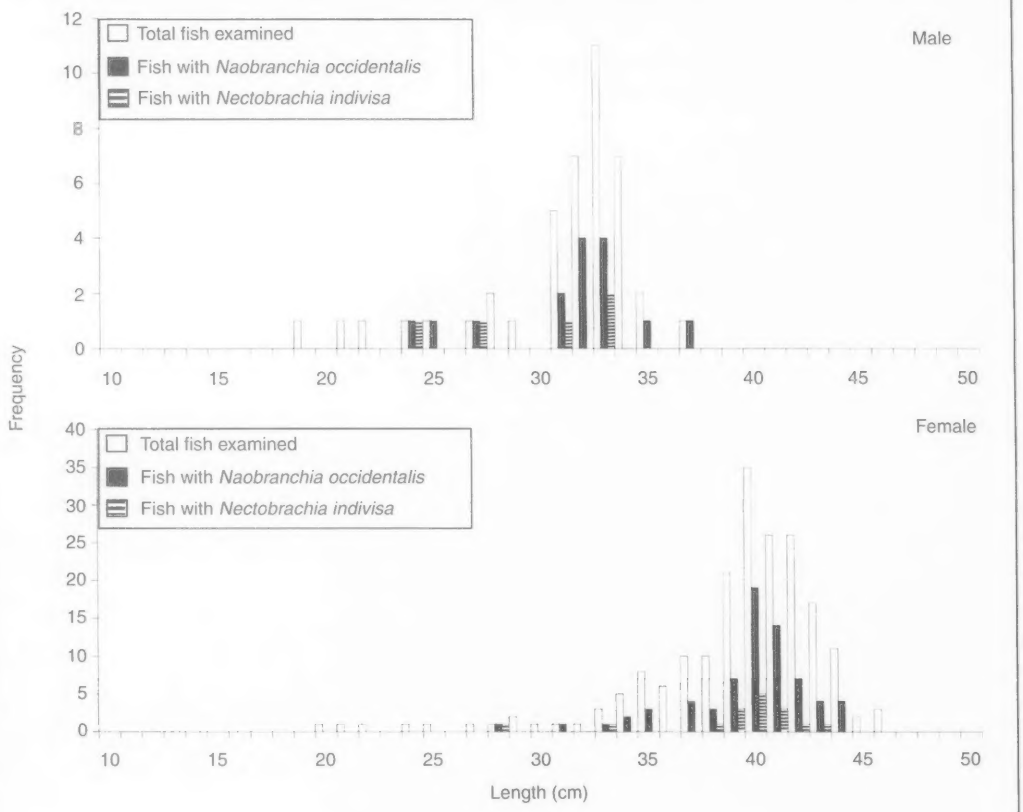

Figure 5

Length frequency of male and female northern rock sole examined for parasites from the Aleutian Islands. Numbers of fish infested with one parasite species added to those infested with the other parasite species may exceed the total because several fish were infested with both parasite species.

from the Aleutian Island samples had white gill filaments. Because of this observation and the apparent preference of *Nectobrachia indivisa* for northern rock sole, we speculate that the white gill filaments in the northern rock soles from the Gulf of Alaska survey may have been caused by heavy infestation with *N. indivisa*.

The decreased weight at length of parasitized male northern rock soles from the Gulf of Alaska indicates a possible effect of infestation. It is interesting to note that northern rock soles from both areas, which were infested with one parasite, had an increased chance of also being infested by the other parasite. Either some northern rock soles are more susceptible to infestation by both parasites, or infestation by one parasite increases the likelihood of infestation by the other species. Because infestation of southern rock soles by *Nectobrachia indivisa* was independent of infestation by *Naobranchia occidentalis*, it is possible that southern rock sole may be resistant to infestation by both parasite species.

Apparently *Naobranchia occidentalis* infests smaller northern than southern rock sole; thus, much of the southern rock sole population may be unavailable to successful infestation by this parasite. This size-dependent prevalence may be related to the grasping method of attachment of *N. occidentalis*; thus, its ability to infest rock sole may be related to the diameter of the gill filaments. Cressey et al. (1983) proposed a similar mechanical limitation for female pseudocycnids that grasp the gill filament in scombrids by partially encircling it with the lateral lobes of their cephalon. They suggested that hosts must reach a minimum size before the gill filament is large enough for the parasite to achieve a firm grip. Roubal and Graham (1999) noted that the smallest fish in their study were not infested with *Naobranchia variabilis*, which attaches to gill filaments in a similar manner as *N. occidentalis*, and suggested it was because those fish simply had not been encountered by a parasite. They did not suggest any sort of mechanical limitations to successful infestation because the

parasite larvae are apparently sufficiently small (Roubal[3]). Both Cressey et al. (1983) and Roubal and Graham (1999) noted that the largest adult parasites were found on the largest fish— a finding that suggests that the gill filaments of smaller fish may be less suitable for infestation.

Nectobrachia indivisa also selectively infested larger northern rock sole but rarely infested southern rock sole, suggesting an apparent species preference. Because *N. indivisa* attaches by means of a bulla permanently embedded near the end of a gill filament, it seems less likely that this parasite would be limited by mechanical restrictions such as the diameter of the gill filament. The parasite *Salmincola californiensis*, which also attaches to its host by means of a bulla (Kabata and Cousens, 1972), seemed to be dependent on its sockeye salmon (*Oncorhynchus nerka*) host reaching a large size before the gill filaments became the preferred site of attachment (Kabata and Cousens, 1977). Perhaps *N. indivisa* is able to infest northern rock sole successfully only after the fish reach a certain size.

We did not perform histological analysis of gill filaments to determine differential damage caused by infestation of *Naobranchia occidentalis* and *Nectobrachia indivisa*. Roubal (1999) determined that damage caused by *Naobranchia variabilis* was restricted to the infested gill filament and was minor. Kabata (1984) noted that naobranchids only partially compress the gill filament, do not completely restrict blood flow, and do not cause whitening of gill filaments. Roubal (1999) also determined that *N. variabilis* live by feeding on the blood supply and not by grazing the tissue, as do lernaeopodids. Kabata and Cousens (1977) reported macroscopic observations of significant atrophy and tissue reaction to as much as one-third of the gill filament surface area of juvenile sockeye salmon due to the presence of *S. californiensis*. This type of damage is consistent with our macroscopic observations of the white gills of northern rock soles seen early in the Gulf of Alaska survey. Kabata and Cousens (1977) also reported on microscopic observations of gill filament damage, sometimes including proliferation of the gill epithelium, hypertrophy of epithelial cells, fusion of adjacent filaments, thickening of filament walls, blood blisters, and erosion of epithelial cells as the oral apparatus of the *S. californiensis* scrapes them for ingestion.

Margolis and Arthur (1979), Kabata and Whitaker (1984), and Kabata (1988) all reported that both *Naobranchia occidentalis* and *Nectobrachia indivisa* occurred on rock soles in Pacific Canadian waters, prior to the determination that there are two species of rock sole in this area (Orr and Matarese, 2000). Neither Moles (1982) nor Love and Moser (1983) reported these parasites from rock soles from Alaskan waters and U.S. west coast waters, respectively. Our study reported new host records for *Acanthochondria vancouverensis* and *Haemobaphes diceraus* on northern rock sole.

The apparent preference of both parasites for the northern rock soles is supported by the conclusion of Orr and Matarese (2000) that northern and southern rock soles are two distinct species. Possible differences in the ecology of these newly described rock sole species, such as food habits, growth rates, habitats, spawning seasons and locations, nursery grounds, and seasonal and ontogenetic migrations might also account for the differential parasitism that we observed. It is not known if parasite prevalence and intensity is related to differences in the ecology and behavior of these closely related species, or related to differences in their anatomy or physiology. As more research is done on these species, based on the work of Orr and Matarese (2000), more potential differences will be determined.

[3] Roubal, F. R. 1999. Personal commun. Department of Parasitology, The University of Queensland, Brisbane 4072, Queensland, Australia.

Acknowledgments

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Size distribution of southern bluefin tuna (*Thunnus maccoyii*) by depth on their spawning ground

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Indonesian and Japanese longline vessels catch different-size southern bluefin tuna (*Thunnus maccoyii*) on their spawning ground in the Indian Ocean south of Bali. The length distributions of southern bluefin tuna (SBT) caught by Japanese longline are markedly smaller than those caught by the Indonesians (Davis et al.[1]; Itoh[2]). Both measurement error and misidentification of small SBT as bigeye tuna (*Thunnus obesus*) in the Indonesian catch data have been suggested as causes of this discrepancy (Suzuki and Nishida[3]), but neither has been substantiated. Japanese vessels target bigeye tuna by using deep longline sets (Itoh[2]), whereas most Indonesian vessels target yellowfin tuna (*Thunnus albacares*) by using shallow longline sets (Davis et al., 1995). The difference in types of longline sets raises the possibility that SBT on the spawning ground are segregated by size with depth.

Three types of boats operate in the Indonesian fishery (Davis et al., 1995). Deep longline boats (generally >50 tonnes) use multifilament mainlines that are set deep. Mini (<20 tonnes gross weight) and regular longline boats (20–50 tonnes) use monofilament mainlines and generally make shallow longline sets. However, the depth at which the lines fish varies considerably because they carry live or frozen baits according to different phases of the moon, and both the number of hooks and their placement on the catenary between floats changes. Prediction of fishing depth based on catenary geometry, line length, and distance between floats (Yoshihara, 1954) differs significantly from actual depth fished (Saito, 1973; Nishi, 1990; Boggs, 1992). In this fishery, the number of hooks between floats is recorded (Davis et al., 1999), but this parameter alone is a poor indicator of the depth of fishing.

Using hook timers, Boggs (1992) determined depth at the time of hooking. He found that bigeye catch rates peaked at 360–400 m and 8–10°C (temperature), but were still high at 200–360 m. Bigeye tuna have a shallower distribution at night (modal depth of 80 m) than during the day (220 m) (Holland et al., 1990). However, on the SBT spawning ground, longline setting starts at about 06:00 h and hauling starts at about 14:00 h (Davis[4]); therefore most bigeye tuna would be caught during the day when they are deeper.

The preferred depths of bigeye tuna vary regionally depending on thermocline structure, but lie within 10° and 15°C (Hanamoto, 1986; Mohri et al., 1996) and where $O_2 > 1$ mL/L (Hanamoto, 1986). These temperatures occur at 180–400 m on the SBT spawning ground (Yukinawa and Miyabe, 1984; Yukinawa and Koido, 1985; Yukinawa, 1987). Yellowfin tuna, on the other hand, are found in warmer waters and are mainly caught at depths of 40–230 m (Suzuki and Kume, 1982; Yang and Gong, 1988; Boggs, 1992). The proportion of bigeye to yellowfin tuna might therefore be used as a proxy for the depth of fishing in the Indonesian longline fishery. In our study we used this depth proxy to investigate whether there is size partitioning by depth of SBT on the spawning ground, and what underlying biological processes might be involved.

Methods

We used catch data obtained from 15,882 Indonesian longline landings monitored at export processing factories at the Port of Benoa, Bali, from 1992 to 1999 (Davis et al., 1995; 1999). About 65% of the SBT in these landings were measured (fork length in cm). Fewer high-grade export tuna (30%) were measured than low-grade tuna (89%) because the former were immersed in an ice slurry immediately after grading, leaving little opportunity for measurement. Grading, however, was not dependent on size. There was no significant difference in the length distributions of 102 export tuna and 102 low-grade tuna from 20 landings in which all tuna were measured (Kolmogorov-Smirnov two sample test, P=0.22).

[1] Davis, T. L. O., J. H. Farley, and S. Bahar. 1996. Catch monitoring of the fresh tuna caught by the Bali-based longline fishery. Commission for the Conservation of Southern Bluefin Tuna scientific meeting, 26 August–5 September 1996, Hobart, Australia, Rep. CCSBT/SC/96/6, 26 p. CSIRO Marine Laboratories, PO Box 1538, Hobart, Tasmania 7001, Australia.

[2] Itoh, T. 1997. Longline survey in southern bluefin tuna spawning ground. Commission for the Conservation of Southern Bluefin Tuna scientific meeting, 28 July–8 August 1997, Canberra, Australia, Rep. CCSBT/SC/97/12, 4 p. CSIRO Marine Laboratories, PO Box 1538, Hobart, Tasmania 7001, Australia.

[3] Suzuki, Z., and T. Nishida. 1997. Comparison of information on the catch and size of fish in the spawning ground of southern bluefin obtained from Indonesian and Japanese longline fisheries. Commission for the Conservation of Southern Bluefin Tuna scientific meeting, 28 July–8 August 1997, Canberra, Australia, Rep. CCSBT/SC/97/13, 8 p. CSIRO Marine Laboratories, PO Box 1538, Hobart, Tasmania 7001, Australia.

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Table 1

Distribution (%) of length groups (10-cm intervals) of southern bluefin tuna across bigeye tuna (BE) indices (Pearson chi-square=516, n=8416, df=24, <0.001).

	BE indices						
Length (cm)	0.0–0.2	0.2–0.4	0.4–0.6	0.6–0.8	0.8–1.0	Total no.	Total
140–149	13.3	6.7	13.3	26.7	40.0	15	100.0
150–159	2.8	10.1	17.0	18.6	51.4	247	100.0
160–169	8.7	15.4	19.5	24.5	31.8	1019	100.0
170–179	12.7	25.7	20.8	20.8	20.0	2442	100.0
180–189	17.9	26.6	18.5	19.3	17.8	3520	100.0
190–199	27.0	23.7	18.9	14.7	15.7	990	100.0
200–209	35.9	21.8	19.6	10.9	12.0	184	100.0
No. of landings	2100	3585	3876	4421	1900		

For each landing we calculated a bigeye (BE) tuna index as

$$BE\ index = Weight\ of\ bigeye / (weight\ of\ bigeye + weight\ of\ yellowfin).$$

This equation was used as a proxy for the depth of fishing, with an index of 1 = deep and 0 = shallow. Landings were grouped into one of five levels of this index, i.e. 0–0.2, 0.2–0.4, etc., and then the length-frequency distributions of SBT within landings at each level were compared.

In order to investigate patterns of distribution of fish size with depth, we grouped fish into 10-cm length classes and calculated their relative abundance across the five levels of the BE index. Because of uneven sampling with depth, the number of fish in each BE index were first weighted inversely by the effort (number of landings) at each level of the index.

The ovaries of 475 SBT were collected during monitoring from 1992 to 1995. These were examined histologically for evidence of recent or imminent spawning (Farley and Davis, 1998). Spawning fish were classed as those having spawned less than 24 hours previously (postovulatory follicles present in ovary), or about to spawn that day (ovaries containing oocytes at migratory nucleus or hydrated stage). Postspawning SBT were identified by the proportion and type of atretic oocytes present (see details in Farley and Davis, 1998). Nonspawning SBT were mature fish on the spawning ground that were neither spawning nor postspawning individuals.

Chi-square contingency analyses were used to test for differences in length classes of SBT, and for differences in the proportion of spawning and nonspawning SBT at different levels of the BE index (the proxy for depth).

Results

The length-frequency distribution of SBT caught at five levels of the BE index shows a trend of increased proportions of small SBT with an increase in this index (Fig. 1). Fish <165 cm ranged from 3.3% of catch at an index <0.2 to 15.7% at a index >0.8.

Chi-square contingency analyses indicated significant differences in the proportion of length classes with the BE index (Table 1, Fig. 2). The chi-square test ignores the ordered and continuous nature of the categories, making it less powerful than it could be. However, we obtained a highly significant test result despite this weakness, reflecting how strong the size-with-depth patterns are. The smaller length classes (150–169 cm) were better represented in the deep catches (BE index >0.8) than they were in the shallow catches (BE index <0.2). Conversely, the larger length classes (190–209 cm) were better represented in the shallow catches (BE index <0.2) than they were in the deep catches (BE index >0.8). Smaller fish were more likely to be caught in the deepest sets, which target bigeye, whereas the bigger fish were more likely to be caught in the shallow sets. Significantly, there is a systematic change in depth distribution with size over the whole size range of SBT that occur on the spawning ground. This pattern is very clear when comparing the proportion of fish caught in shallow (BE index of 0.0–0.2 or 0.0–0.4) versus deep (BE index of 0.8–1.0 or 0.6–1.0) sets for each length class. The proportion of SBT caught at the surface increases with size (Fig. 3).

The proportion of spawning and nonspawning fish (based on the subset of histological data) was then determined for each level of BE index (Fig. 4). Chi-square contingency analyses indicated significant differences in the proportions (Table 2). Spawning fish were better represented in the shallow catches than in the deep catches. Conversely, nonspawning fish were better represented in the deep catches than in the shallow catches. There were insufficient numbers of SBT in the smaller size classes (only seven SBT<160 cm) to use the histology data to examine directly the relation between size and proportion of spawning fish or spawning frequencies. Because spent fish were rarely encountered on the spawning ground, Farley and Davis (1998) concluded that they move south soon af-

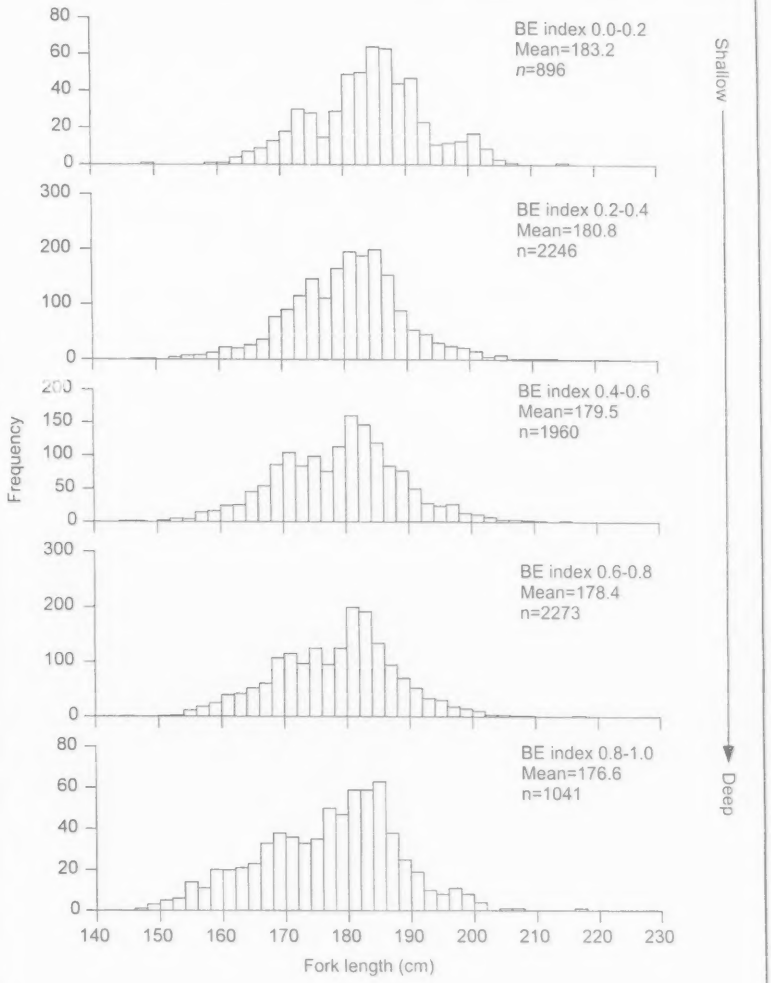

Figure 1

Length-frequency distribution (2-cm intervals) of southern bluefin tuna in landings by bigeye tuna index—a proxy for fishing depth.

ter spawning. However, the two spent fish detected were in landings with a BE index >0.9.

Discussion

There is a systematic change in depth distribution with size over the whole size range of SBT caught on the spawning ground. This pattern is clear, even though the BE index may only represent a crude approximation of depth. Deep longline catches are often contaminated by surface catches—10% of bigeye tuna are caught when hooks are not at settled depths (Boggs, 1992). Also, both SBT (Gunn et al.[5]; Davis and Stanley[6]) and bigeye tuna (Holland et al., 1990) might be caught outside their preferred depth as they regularly traverse the water column.

[5] Gunn, J. S., T. Polacheck, T. L. Davis, M. Sherlock, and A. Betlehem. 1994. The application of archival tags to study the movement, behaviour and physiology of southern bluefin tuna, with comments on the transfer of the technology to groundfish research. ICES CM 1994/Mini: 21, 23 p. [Mimeo.]

[6] Davis, T. L. O., and C. A. Stanle. 2001. In prep. Vertical and horizontal movements of southern bluefin tuna, *Thunnus maccoyii*, in the Great Australian Bight observed by ultrasonic telemetry.

The pattern of size distribution with depth is mirrored by the pattern of spawning and nonspawning with depth. Both smaller and nonspawning SBT are more abundant at depth, whereas both larger and spawning SBT are more abundant near the surface. The vertical distribution of SBT larvae suggests that SBT spawn at the surface (Davis et al., 1990), as do caged Atlantic bluefin tuna (*Thunnus thynnus*) (Fushimi et al., 1998). Surface-water temperatures on the spawning ground usually exceed 24°C (Yukinawa and Miyabe, 1984; Yukinawa and Koido, 1985; Yukinawa, 1987). These warm surface waters may be necessary for the survival of their eggs and larvae, but adult SBT normally feed in colder water (often as low as 5°C [Olson, 1980]). Temperatures of 10°–15°C preferred by bigeye tuna (Hanamoto, 1986; Mohri et al., 1996) may offer more favorable conditions for nonspawning SBT and explain their strong association with high BE indices on the spawning ground.

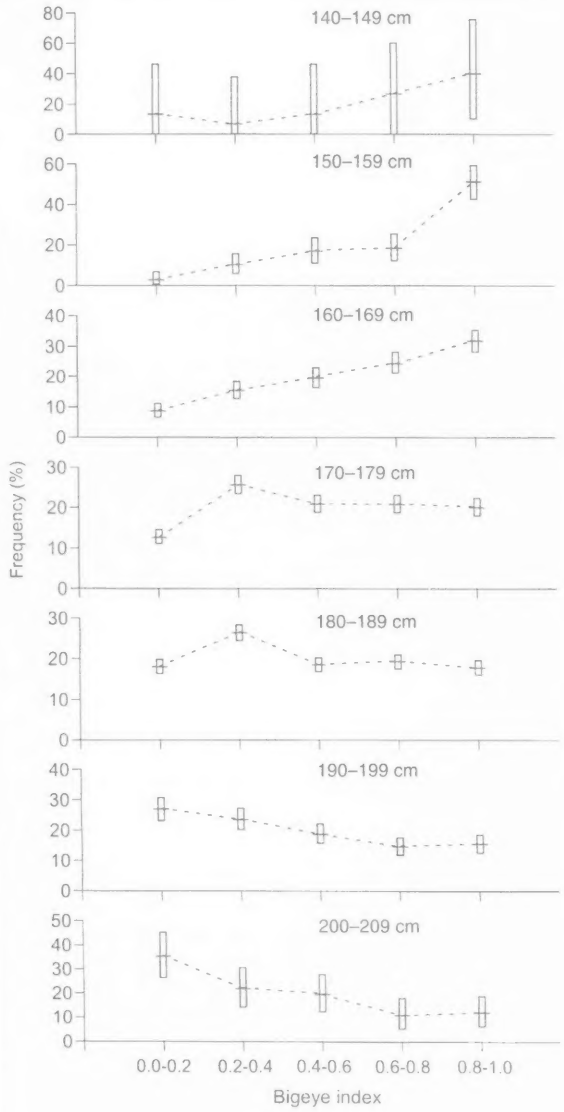

Figure 2

Proportion of each 10-cm length group in landings by bigeye tuna (BE) index. Vertical bars represent 95% confidence limits of the mean based on an approximation by Bailey (1980).

Previous studies have shown that yellowfin tuna caught by purse seine and handline have higher gonadosomatic indices than yellowfin caught by longline (Hisada, 1973; Suzuki, 1988; Koido and Suzuki, 1989). Histological studies have found that yellowfin tuna catches from purse-seine sets and shallow (Taiwanese-style) longline sets have a higher proportion of actively spawning fish than catches from deep (Japanese-style) longline sets (Itano[7]). Thus, spawning fish are more likely to be caught near the surface and nonspawning fish are more likely to be caught in deeper water.

The biological basis for size partitioning with depth could be that large fish spawn more frequently than small fish and, therefore, bigger fish will be caught at the surface more often than smaller ones. Spawning frequency is known to increase with size in female yellowfin tuna (Schaefer, 1998) but could not be determined for SBT. The pattern of size distribution may reflect recruitment into spawning. However, this hypothesis is unlikely because histological examination of ovaries indicated that all SBT caught on the spawning ground were mature i.e. had advanced yolked oocytes (Farley and Davis, 1998), although this does not preclude the possibility that they might not be ready to spawn. The most likely reason for size partitioning is that the spawning frequency or the proportion of time spent spawning to time spent in a nonspawning condition increases with size.

If the ability to tolerate higher than preferred water temperatures improved with fish size, then this would facilitate longer spawning episodes or more extensive feeding in shallow waters, both of which would produce the observed pattern of size distribution with depth. Although the ability to conserve heat in cold waters may increase with size in SBT, it is not clear what size-dependent processes might be involved in avoiding overheating at high ambient temperatures.

We do not understand the temporal and spatial scale of vertical movements of SBT on the spawning grounds in relation to spawning and feeding, nor

[7] Itano, D. G. 2000. The reproductive biology of yellowfin tuna (*Thunnus albacares*) in Hawaiian waters and the western tropical Pacific Ocean: project summary. SOEST (School of Ocean and Earth Science and Technology) 00-01, JIMAR (Joint Institute for Marine and Atmospheric Research) Contribution 00-328, 69 p. Univ. Hawaii, 1000 Pope Road, MSB 312, Honolulu, HI 96822-2336, US.

Table 2

Percentage of spawning and nonspawning southern bluefin tuna caught at different bigeye indices (Pearson chi-square=24.1, n=326, df=4, P<0.001).

	BE index					
	0.0–0.2	0.2–0.4	0.4–0.6	0.6–0.8	0.8–1.0	Total no.
Spawning	85.5	71.4	80.8	56.4	56.3	227
Nonspawning	14.5	28.6	19.2	43.6	43.7	99

how these might change with fish size. This behavioral information is needed in order to interpret the patterns presented in our study and might best be achieved by pop-up satellite archival tagging.

Because SBT aggregate by size and depth on the spawning ground, it is necessary to account for their distribution when determining the age and size structure of the spawning stock. This is especially important when evaluating time series of size and age distributions in a fishery where there have been shifts in targeting between yellowfin and bigeye tuna. In the absence of reliable information on the depth of fishing, the most practical way of doing this in the Indonesian fishery would be to inversely weight the effort directed at the different levels of the BE index. The determination of spawning frequency should also take into account longline fishing strategies because it is likely that spawning frequency is affected by fish size and because samples will be caught within or outside the spawning depth.

If the increase in the proportion of SBT at the surface with size is due to spawning activity, then this feature will affect the contribution different size fish make to total annual egg production. A lower spawning frequency, coupled with an exponential relationship between length and batch fecundity (Farley and Davis 1998), would mean that individual small, but mature, fish make a relatively small contribution to total annual egg production. When making stock projections, it may therefore be more appropriate to adopt a parameter that reflects size at mean annual egg production rather than the currently accepted parameter of mean size at first maturity. Further histological research on the reproductive dynamics of small fish is required to better define these parameters. Small fish were rarely caught when the histological work of Farley and Davis (1998) was carried out in 1992–95 but they have become more abundant in recent years (Davis et al.[8]) making such a study possible.

[8] Davis, T. L. O., S. Bahar, N. Naamin, and J. H. Farley. 1998. Catch monitoring of the fresh tuna caught by the Bali-based longline fishery. Commission for the Conservation of Southern Bluefin Tuna scientific meeting, 23–31 July 1998, Shimizu, Japan, Rep. CCSBT/SC/9807/6, 17 p. CSIRO Marine Laboratories, PO Box 1538, Hobart, Tasmania 7001, Australia.

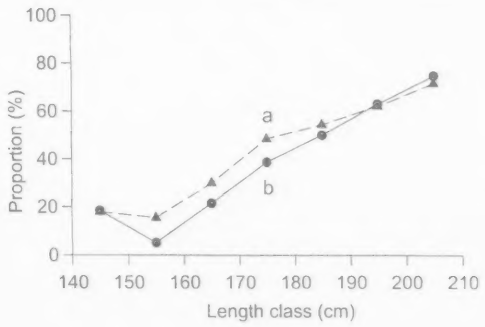

Figure 3

Proportion of southern bluefin tuna caught at the surface by length class. Estimates were calculated by using (a) bigeye tuna (BE) index of 0.0–0.2 and 0.8–1.0 and (b) BE index of 0.0–0.4 and 0.6–1.0.

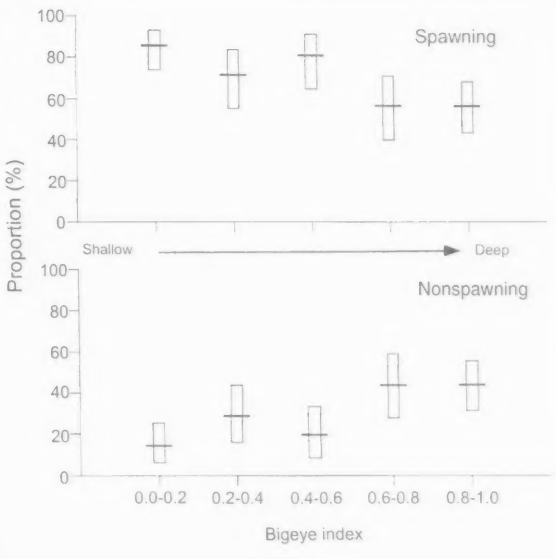

Figure 4

Proportion of spawners and nonspawners in landings by the bigeye tuna index.

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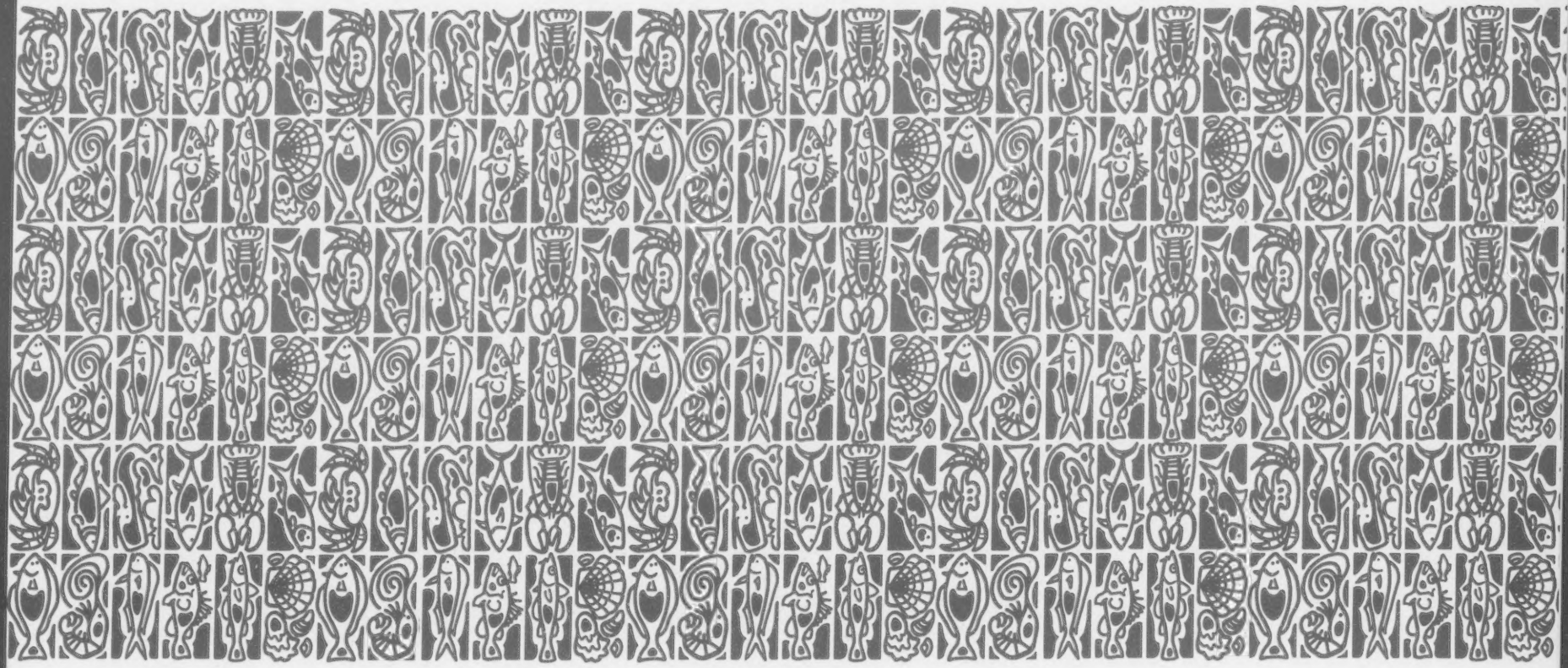
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